

Transactions of the Royal Society of South Australia Incorporated

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A REVIEW OF THE AUSTRALIAN MOTH GENUS THALAINA (LEPIDOPTERA: GEOMETRIDAE: ENNOMINAE)

BY P. B. MCQUILLAN

Summary

The moth genera *Thalaina* Walker, *Thalainodes* Lower and *Macqueenia* Turner are reviewed. New evidence has resulted in an expansion of the concept of *Thalaina* to include the other genera in its synonymy. Nine species are reviewed and *T. kimba* sp. nov., is described from the mallee areas of South Australia and New South Wales. Immature stages, foodplants, flight activity and distribution of the various species are recorded where known. The genus has adapted successfully to most major habitats in the southern half of Australia wherever their food plants (*Acacia* and *Cassia*) are established.

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by P. B. McQUILLAN*

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Introduction

This is the first of a proposed series of taxonomic studies on the ennomine geometrids of southern Australia. It reviews the taxonomic status and known biology of a distinctive group of autumn-flying moths previously referred to *Thalaina* Walker, *Thalainodes* Lower and *Macqueenia* Turner.

All the species are large, strikingly patterned, nocturnal moths with distinctive larvae. Not surprisingly, all four species found in coastal eastern Australia were described by 1865. Residing at Broken Hill O. B. Lower discovered and described three inland species between 1900 and 1902, and his series of two of them constitute most of the specimens available for study. An apparently localised species was discovered in the 1930's at Millerran, southern Queensland by J. Macqueen and is still very poorly known. In the 1960's and early 1970's a few specimens of a widespread central Australian species were collected and subsequently described in 1972. Similarly, concentration of collecting in the semi-arid areas of southern Australia during late autumn by CSIRO collectors over the last ten years has made available a good series of another new species described here.

Methods

The following abbreviations are used for collections: AM = Australian Museum, Sydney; ANIC = Australian National Insect Collection, CSIRO, Canberra; BMNH = British Museum (Natural History), London; NMV = National Museum of Victoria,

Melbourne; PBMcQC = P. B. McQuillan collection, Adelaide; QM = Queensland Museum, Brisbane; SAM = South Australian Museum, Adelaide; TDA = Tasmanian Department of Agriculture, Hobart; TMAG = Tasmanian Museum and Art Gallery, Hobart; UQ = University of Queensland, Brisbane; WAM = Western Australian Museum, Perth.

Abbreviations of the names of collectors are: PA = P. Aitken, FMA = F. M. Angel, EA = E. Ashby, WBB = W. B. Barnard, RB = R. Beresford, TB = T. Blackburn, TGC = T. G. Campbell, DHC = D. H. Colless, IFBC = I. F. B. Common, JRC = J. R. Cunningham, JWD = J. W. Davies, EJD = E. J. Duffigan, EDE = E. D. Edwards, BE = B. Evans, RHF = R. H. Fisher, CWF = C. W. Frazier, NG = N. Geary, GCLG = G. C. L. Gooding, GHH = G. H. Hardy, RJH = R. J. Hardy, JH = J. Harslett, CCI = C. C. Ives, WK = W. Kleezaj, LEK = L. E. Koch, LRK = L. R. Kurtze, AML = A. M. Lea, RL = R. Lewis, OBI = O. B. Lower, GL = G. Lyell, NMtF = N. McFarland, KJMcK = K. J. McKie, JM = J. Macqueen, PBMcQ = P. B. McQuillan, WLM = W. L. May, VHM = V. H. Minchin, BM = B. Mollison, GBM = G. B. Monteith, JGM = J. G. Morris, TN = T. Newberry, LJN = L. J. Newman, KRN = K. R. Norris, HP = H. Pelz, RJP = R. J. Priest, PR = P. Ranford, LMR = L. Mosse-Robinson, VJR = V. J. Robinson, ALR = A. L. Rogers, RS = R. Straatman, JJHS = J. J. H. Szent-Ivany, JGOT = J. G. O. Tepper, HST = H. S. Thirkell, LBT = L. B. Thorn, NBT = N. B. Tindale, HU = H. Udell, MSU = M. S. Upton, MMHW = M. M. H. Wallace, RW = R. Went, JOW = J. O. Wilson, RGW = R. G. Winks, FWJ = F. Wood-Jones.

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Numbers prefixed by "G" accompanying the descriptions of immature stages relate to code numbers of specimens in the McFarland larval collection housed at the S.A. Museum, Adelaide; see McFarland (1979) for full details.

Genus *THALAINA* Walker

Thalaina Walker 1855, p. 659; Type species *Thalaina klenaea* Walker (= *Thalaina selenaea* (Doubleday)), by subsequent designation by Fletcher 1979, p. 202.

Absyrtes Guenée, 1857, p. 226; Type species *Absyrtes magnificaria* Guenée, by subsequent designation by Fletcher 1979, p. 1.

Thalainodes Lower 1902, p. 231; Type species *Amelora tetraclada* Lower, by subsequent designation by Turner 1919 p. 386; *syn. nov.*

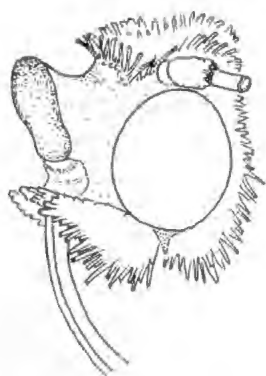
Macqueenia Turner 1947, p. 101; Type species *Macqueenia chionoptyla* Turner, by monotypy; *syn. nov.*

Adult: Medium sized, moderately robust, nocturnal moths; wing expanse 34–54 mm. Colour

pattern basically white with or without darker geometrical markings.

Head (Figs 1, 2) with vestiture of crown thick, hair-like slightly roughened; frons well rounded (fairly convex), clothed in scales, or nearly naked and bearing series of shallow transverse ridges beneath large sclerotized median projection; labial palp short, slightly correct, second segment with projecting scales below, terminal segment very short; haustellum fully developed and functional; antenna in male laminate or strongly bipectinate, in female filiform; compound eye large, globular, without hairs; ocelli absent; chaetosemata present.

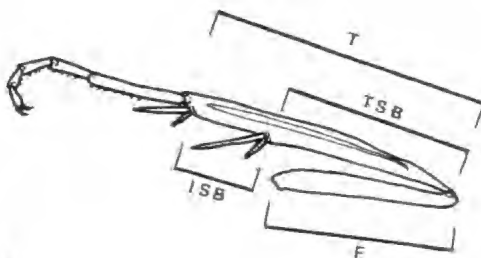
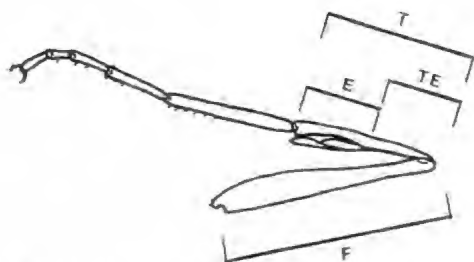
Thorax clothed with mixed hair-like and spatulate vestiture; forewing triangular, apex often subfalcate, in male without fovea, pattern usually white with ochreous geometrical pattern or rarely suffused darker; Sc and R_1 anastomosed, R_2 anastomosed with R_{3+4} to



1



2



3

Figs 1–2. Heads of *Thalaina* spp. 1. *T. tetraclada*; 2. *T. macfarlandi*.

Fig. 3. Fore and hind leg of *Thalaina* sp. E—length of epiphysis; F—length of femur; ISB—distance between spur bases; T—length of tibia; TE—distance from top of tibia to top of epiphysis; TSB—distance from top of tibia to top of spur base.

TABLE 1. Comparison of some mean ratios from leg measurements of *Thalaina* species (see fig. 3 for abbreviations).

	n	Fore leg			Hind leg		
		F/T	TE/T	E/T	F/T	TSB/T	ISB/T
<i>selenasa</i> ♂	3	1.51	0.56	0.45	0.68	0.66	0.28
<i>angulosa</i> ♂	3	1.50	0.53	0.45	0.66	0.67	0.28
<i>clara</i> ♂	3	1.75	0.60	0.48	0.68	0.64	0.33
<i>inscripta</i> ♂	3	1.77	0.61	0.44	0.71	0.67	0.28
<i>allochroa</i> ♂	3	1.51	0.28	0.46	0.78	0.67	0.27
<i>paronycha</i> ♀	2	1.59	0.29	0.35	0.86	0.69	0.22
<i>kimba</i> ♂	2	1.48	0.40	0.38	0.81	0.73	0.24
<i>chlonoptila</i> ♂	2	1.60	0.51	0.55	0.68	0.66	0.27
<i>tetraclada</i> ♂	3	1.46	0.49	0.51	0.66	0.67	0.28
<i>macfarlandi</i> ♂	1	1.17	0.43	0.34	0.76	0.72	0.24

form an areole, R_2 stalked with R_{3+4} . M_2 often arising nearer to M_1 than to M_3 ; hind-wing white, sometimes with darker markings, cell rather long; femora smooth-scaled, posterior tibiae in male slightly dilated, fore tibiae with epiphysis, sometimes with apical hook, mid and hind tibiae with spurs well developed (for leg measurements, see Table 1).

Abdomen with comb on segment 3 in male weakly to moderately developed.

Male genitalia with uncus simple, slender, apically acute; socii well developed, gnathos simple, slender, with small median recurved spine or group of small spines at apex; juxta broadly rectangular or shield-shaped; furca usually long, bifid; cristate hairs well developed; valva elongate, slightly spatulate; aedeagus tubular, slightly curved with pointed apex and oblique distal orifice, cornuti usually a series of stout, often compound spines.

Female genitalia with papillae anales densely hairy, bases of hairs set in conical projections; apophyses posteriores about 1.4 times as long as apophyses anteriores; sterigma broadly cup-shaped; ductus bursae long, with parallel sides, weakly sclerotized, in diameter about $\frac{1}{2}$ that of corpus bursae, its posterior part usually with ring of longitudinal sclerotized striations; corpus bursae ovoid, without signa.

Egg broadly ovate, with or without darker marking.

First instar larva with head capsule brown, without pattern; body pale yellow; setae extremely long and quite stout; setae XD and D on prothorax on a lightly sclerotized plate; anterior humps on prothorax lacking. Abbreviated prolegs present on A4 and A5; crotchets arranged in complete circle on A4 and A5 (numbering about 12) and in half circles on A6 and claspers.

Final instar larva with head capsule green to yellow-green with numerous small brown blotches across vertex; labrum deeply emarginate; body fairly robust, pale green to dull green with at least a whitish lateral stripe; cuticle smooth; setae short and fine; prothorax somewhat swollen and produced into two anterior dorso-lateral fleshy projections; abbreviated prolegs present on A4 and A5; crotchets in $\frac{3}{4}$ circle on A4, in $\frac{5}{6}$ circle on A5 and $\frac{1}{2}$ circle on A6 and claspers, uniorbital on A4–A6 but tending to be biordinal on claspers of some species; numbers of crotchets range: 13–21 on A4, 14–29 on A5, 25–37 on A6 and 28–48 on claspers; length 23–41 mm, width 4.5–5.5 mm; head capsule width 2.3–3.5 mm. The larvae are foliage mimics, being basically green in colouration with pale lateral and ventral stripes. Those species feeding on bipinnate *Acacia* usually have pale dorsal stripes and more mottled colouration.

Pupa dark brown to orange-brown; smooth, anterior margin of A10 dorsally with 2–4 widely rounded teeth; cremaster hooks 2 or 6–8; length 11–17 mm, width 5–6 mm. Aestivates in loose cocoon incorporating detritus, beneath litter or in the soil.

Flight Period: Mostly late summer to late autumn; flight periods for individual species range from less than four to more than twelve weeks. Figure 18 shows flight periods for species represented in collections by over 20 specimens with full data.

Distribution: Australia, south of about latitude 24°; see figs 49–51.

Key to adults:

1. Frons more or less naked, with sclerotized median projection 2
- Frons covered with hair-scales, without median projection 6
2. Forewing satiny-white with sharply defined orange-brown or ochreous brown markings 3
- Forewing mostly pale ochreous-grey or grey 5
3. Forewing with stripe along middle one-third of costa 4
- Forewing without stripe along middle one-third of costa *macfarlandi* (Wilson)
4. Forewing with oblique stripe from near mid termen to costal streak at three-quarters *paronycha* (Lower)
- Forewing without stripe connecting termen and costa as above *tetraclada* (Lower)
5. Forewing completely ochreous-grey, minutely speckled with black *allochroa* (Lower)

- Forewing white but heavily marked with broad, suffused grey markings *kimba* sp. n.
- 6. Forewing without markings in disc 7
- Forewing with markings in disc 8
- 7. Hindwing with a large black spot near tornus *chionoptila* (Turner)
- Hindwing without a large black spot near tornus *selenaea* (Doubleday)
- (form *punctilinea* Walker)
- 8. Forewing with short, ochreous brown streaks on M_1 , M_2 , CuA_1 and CuA_2 near termen *inscripta* Walker
- Forewing without markings at extremities of M_1 , M_2 , CuA_1 and CuA_2 9
- 9. Forewing with a relatively straight stripe from tornus to near mid costa or a little below mid costa 10
- Forewing with stripe from tornus not reaching mid costa *angulosa* Walker
- 10. Forewing with diagonal stripe from mid termen to three-quarters of costa *clara* Walker
- Forewing without stripe from mid termen to costa as above *selenaea* (Doubleday)

Thalaina selenaea (Doubleday)

FIGS 4, 14, 18, 19, 29, 39, 49, 52, 53.

Callimorpha selenaea Doubleday 1845, p. 437, pl. 5, fig. 3.

Thalaina selenaea, Meyrick 1892, p. 653; Turner 1919, p. 387.

Thalaina klenaea Walker 1855, p. 660.

Pompeja australiaria Herrich-Schäffer 1855, pl. 60, fig. 333.

Absyrtes australiaria H.Sch. (*magnificaria* Gn.) var. *fortunata* Thierry-Mieg 1899, p. 21.

Absyrtes magnificaria Guenée 1857, p. 226.

Phalaena magnifica Desmarest 1858 syn. nov. (junior objective synonym of *magnificaria* Gn.).

Thalaina punctilinea Walker 1865, p. 228.

Type of *selenaea*: not found in BMNH (D. S. Fletcher, pers. comm.) or any Australian collections.

Types of *klenaea*: lectotype ♀ labelled "*Callimorpha selenaea* H. T. [Hobart Town] Australia 44-105" in BMNH, hereby designated; 1 ♂ paralectotype labelled "46-46" in BMNH, hereby designated.

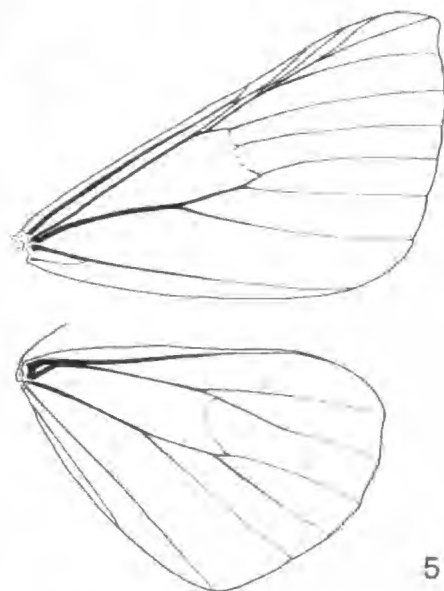
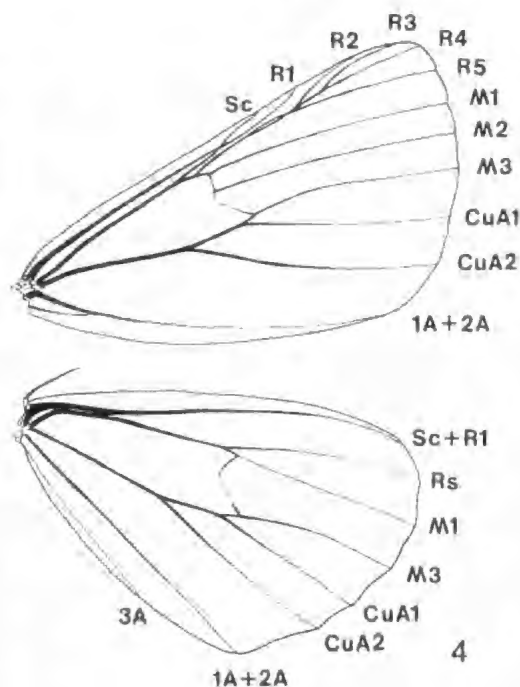
Type of *australiaria*: not found in Zoological Institute, Martin Luther University, Wittenberg, GDR (N. Grosser, pers. comm.).

Holotype ♂ of *australiaria* var. *fortunata* labelled "Typicum specimen: Ex Musaeo Ach. Guenee: Magn. var A Gn.: Ex Oberthur Coll. Brit. Mus. 1927-3" in BMNH.

Type of *magnificaria*: this is the earliest scientific name and formal description of text-fig. 17 p. 5 of Lucas (1857), colloquially

named by him as "*Phalene magnifique*" according to Guenée (1857) 4 ♂, 1 ♀ were in his collection at the time of description; none of these syntypes has been examined.

Type of *magnifica*: Desmarest applied this name to Lucas' unnamed figure; the specimen



Figs 4-5. Venation of *Thalaina* spp. 4. *T. selenaea*; 5. *T. chionoptila*.

on which the figure is based has not been examined.

Type of punctilinea: lectotype ♂ labelled "Tasmania 58-60" in BMNH, hereby designated; 1 ♀ paratype labelled "V.D.L., W.H.S. [or W.W.S.] 43-58" in BMNH, hereby designated.

Adult (figs 52, 53): Head with frons rounded, smoothly hair-scaled, whitish with fuscous band below vertex; vertex with erect hair-scales, bright red-brown; labial palp with terminal segment and apex of second segment fuscous, remainder white; antennae of male laminate. Thorax above greyish white on anterior margin, remainder white, base of wings orange, beneath white; legs white with exterior of fore and mid femur and tibia and all tarsi infuscated; forewing (fig. 4) with costa nearly straight, apex pointed, termen rounded and somewhat sinuate beneath apex, R_1 anastomosed with Sc , R_2 often anastomosed with R_3 to form an areole, ground colour above shining white, red-brown streak along costa from base to one-half thence angled inwards as a narrowly black-margined streak to tornus; similar streak from tornus along inner margin to near base, termen narrowly red-brown, cilia red-brown posteriorly fuscous; hindwings shining white, moderate fuscous subapical blotch, cilia white; forewings beneath shining white infuscated near apex and with costal streak fuscous; hindwings beneath shining white, subapical blotch much enlarged, sharply red-brown above M_1 fuscous below; wing expanse ♂ 48-54 mm, ♀ 52-56 mm.

A common variety of this species (fig. 53) has a reduced costal streak, lacks the diagonal forewing streak and has the streak along the inner margin poorly developed; the subapical hindwing blotch may be reduced or even absent but is fully developed beneath.

Male genitalia (fig. 19) with apex of gnathos with small spine, furca with two prongs of equal length; aedeagus (fig. 29) stout, cornuti of two compound spines subequal in length.

Female genitalia (fig. 39) with corpus bursae elbowed.

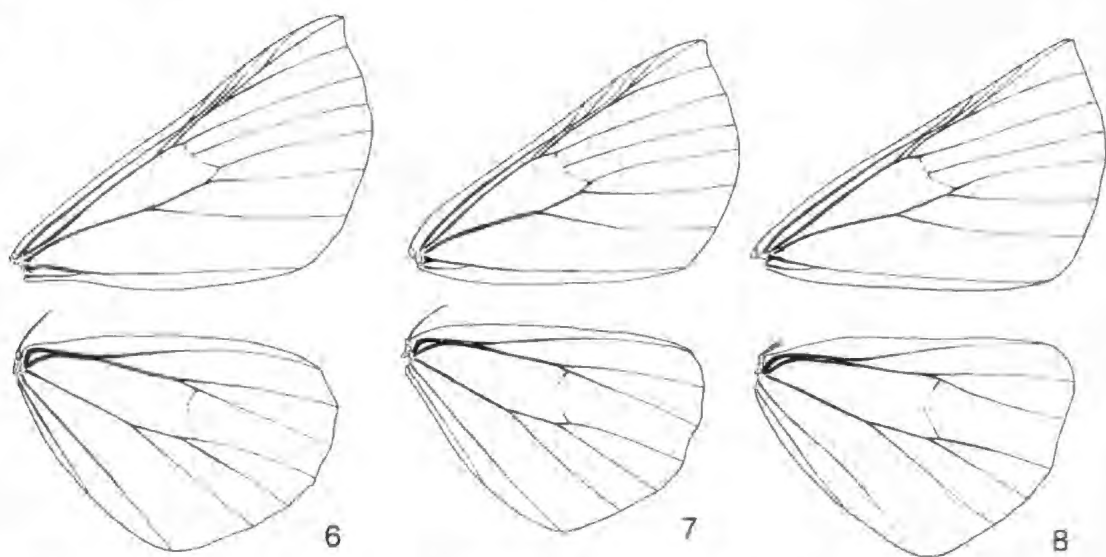
Final instar larva: Head capsule 3.3-3.5 mm wide, pale green with small fuscous blotches across vertex; body green with fine fuscous speckling on anal plate and claspers, fleshy whitish lateral stripe usually present, two white subventral stripes present as blotches adjacent to thoracic legs and continuous from meta-

thorax to A9, incomplete white mid ventral stripe on A1 to A5; crochets 19-21 on A4, 22-29 on A5, 31-37 on A6 and 35-42 on anal claspers, crochets on anal claspers unioordinal; length 38-41 mm, width 5.5-6 mm. Material: G119.

Pupa (fig. 14) mid to dark brown in colour; cremaster hooks 6-8; dorsal anterior margin of A10 with 4 lobes. Material: G119.

Foodplants: *Acacia melanoxylon* R. Br., *A. retinodes* Schlecht.

Specimens examined: 83 ♂ 45 ♀. QUEENSLAND: Brisbane, v. RGW 1 ♀ UQ; Lamington Nat Park, ii., v. WK 2 ♂ UQ; Stanthorpe, iv. 1 ♂ UQ; Toowoomba, iii., iv. EJD 2 ♂ UQ; Wyberba, iii. IFBC 1 ♂ ANIC, NEW SOUTH WALES: Brown Mountain, i. DHC 1 ♂ ANIC; 8 km N of Bungwahl, iii. IFBC & MSU 1 ♂ ANIC; Church Point, v. IFBC 1 ♂ ANIC; Clyde Mtn 800 m, iii. IFBC & MSU 1 ♂ ANIC; 8 km W of Coll's Harbour, v. MSU 1 ♂ ANIC; Depot Beach, iv. IFBC 1 ♂ ANIC; Kangaroo Valley, iii. DHC 1 ♂ ANIC; Katoomba, iii. 1 ♂ SAM; Narara, iv. LMR 1 ♂ ANIC; 5 km SSE of Port Macquarie, v. MSU 1 ♂ ANIC; 2.7 km NE of Queanbeyan 670 m, iv. IFBC 1 ♀ ANIC; 40 km S of Singleton, iii. IFBC 1 ♂ ANIC; Tooloom Scrub, iii. 1 ♂ UQ; 8 km S of Wauchope, iii. IFBC & MSU 1 ♂ 1 ♀ ANIC; Wollongong, iii. VJR 1 ♂ ANIC. AUSTRALIAN CAPITAL TERRITORY: 1.6 km NE of Lee's Spring 1300 m, i. IFBC 1 ♂ 1 ♀ ANIC. VICTORIA: Boronia, iv. 1 ♂ NMV; Castlemaine, iii. 1 ♀ 8 km S of Gellibrand 230 m, ii. IFBC 1 ♀ ANIC; Gisborne, iii., iv. 4 ♂ 3 ♀ ANIC, iv. 68 specimens NMV, i., iii. iv. GL 14 ♂ 4 ♀ SAM; Meenjian, iv. 1 ♀ NMV; Milcham, iv. 1 ♂ 4 ♀ NMV; Moe, iv. 1 ♀ NMV, iii. GCLG 1 ♀ SAM; Mordialloc, v. CCE 1 ♂ ANIC; Mt. Difficult Rd., ii. IFBC 1 ♂ ANIC; Springvale, v. 1 ♀ UQ; Turton's Pass, iii. NBT 5 ♂ 1 ♀ SAM; Wandin, iv. 1 ♀ NMV. TASMANIA: Condominium Creek, ii. 1 ♂ 2 ♀ NMV; Cracroft Crossing, ii. 1 ♀ NMV; Devonport, i. ♂ TDA; Freycinet Nat Park, ii. IFBC & MSU 1 ♂ ANIC; Kelso, 1 ♂ SAM; Kingston, iii., iv. JRC 2 ♂ ANIC, iv. JRC 2 ♀ NMV; Lake Leake 660 m, ii. IFBC & MSU 1 ♂ ANIC; Launceston, iv. 1 ♂ SAM; 16 km W of Maydena, ii. 1 ♂ 4 ♀ NMV; Mt Nelson 200 m, ii., iii. PBMcQ 4 ♂ TDA; Mt Wellington 280 m, i., ii., iii. BM 7 ♂ 4 ♀ ANIC; Ouse, ii., iii., iv. 3 ♂ 1 ♀ TDA; Parenna, King Island, ii. PBMcQ 1 ♂ TDA; Queenstown, v. 1 ♀ NMV; Ridgeway, iv. JRC 1 ♂ 2 ♀ NMV; Roseberry, ii. 1 ♀ ANIC; Sandford, WLM 1 ♂ ANIC; 5 km E of Waratah 660 m, ii. IFBC & MSU 2 ♂ 1 ♀ ANIC; 13 km SW of Waratah 600 m, ii. IFBC & MSU 2 ♂ 1 ♀ ANIC; Zeehan, i. GHH 1 ♂ ANIC, ii. 1 ♂ 1 ♀ NMV. SOUTH AUSTRALIA: Furner, v. 3 ♂ SAM; Naracoorte, 1 ♀ SAM; Yorke Peninsula, iii., iv. JGOT 1 ♂ 1 ♀ SAM.



Figs 6-8. Venation of *Thalaina* spp. 6. *T. angulosa*; 7. *T. clara*; 8. *T. inscripta*.

Distribution: see fig. 49. *Flight Period*: see fig. 18.

Comments: *T. selenaea* is a dimorphic species — one form (var. *punctilinea* Walker) without markings on the forewing and the other with a diagonal bar across the forewing; occasionally a streak along M_3 may also be present (fig. 52). It occurs in habitats in south eastern Australia from open woodland to closed forest in areas of greater than 75 cm annual rainfall and at elevations of 0-800 m. Preferred hosts are large phyllodinous wattles such as *Acacia retinodes* and *A. melanoxylon*. An interesting dwarf population occurs in remnant native forest near Parenna on King Island. This species is the earliest of the genus to appear on the wing, flying from mid January to April.

Thalaina angulosa Walker

FIGS 6, 13, 15, 18, 20, 30, 40, 50, 54.

Thalaina angulosa Walker 1865, p. 289; Meyrick 1892, p. 665; Turner 1919, p. 388.

Holotype ♀ without abdomen, labelled "S. Aust. 61-104" (F. Waterhouse) in BMNH.

Adult (fig. 54): Head with frons rounded, smoothly hair-scaled, whitish-buff; vertex with rough hair-scales, orange; labial palpi with terminal segment and apex of second segment fuscous, remainder of second segment white; antenna of male shortly bipectinate. Thorax above greyish-white becoming whiter posteriorly and on tegulae, orange at base of

wings, white beneath; legs with fore and mid femora and all tarsi infuscated, hind femora and tibiae whitish; forewing (fig. 6) with costa nearly straight, apex produced, termen strongly arched and sinuate below apex, R_1 anastomosed with Sc, ground colour above shining white, a narrowly black-margined rust coloured streak along costa from base to one-eighth costa then extending to mid-discal area where it divides into an upper arm reaching mid termen thence to four-fifths costa and a lower arm extending to tornus thence along the posterior margin to near base, termen narrowly rust coloured, cilia rust posteriorly fuscous; hindwing shining white, a large fuscous subterminal blotch extending from above M_3 to near apex with a narrower extension to anal angle, cilia fuscous on termen from anal angle to five-sixths with remainder white; forewing beneath shining white with upper markings visible, a subapical blotch extending from four-fifths costa to mid termen, orange-rust near costa, remainder fuscous becoming paler apically; hindwing beneath shining white, subterminal blotch as above but less extensive and sharply orange-rust above M_1 ; wing expanse ♂ 40-48 mm, ♀ 42-54 mm. Abdomen white.

Male genitalia (fig. 20) with apex of gnathos bearing a small spine; aedeagus (fig. 30) rather stout, cornuti of two compound spines.

Female genitalia (fig. 40) with ductus bursae swollen proximally.

Egg: Ovoid, greenish, without markings; stimulated to hatch by rainfall. See McFarland 1971, p. 242 for full details. **Material:** G100. **Final instar larva:** Head capsule 3.3 mm wide, greenish with numerous small brown blotches some of which form suffused band across vertex; body bright green with dark speckling on dorsum of prothorax, on anal plate and on claspers; yellowish-white lateral stripe often heavily edged with fuscous on its lower margin, sometimes four faint parallel whitish lines dorsally, two whitish subventral stripes present and incomplete mid ventral stripe on A1 to A6, bases of setae inconspicuous; crochets 16-19 on A4, 20-22 on A5, 29-30 on A6 and 33-38 on anal claspers; length 36-40 mm, width 4.5-5.5 mm. **Material:** G100.

Pupa (fig. 15) mid brown in colour; cremaster hooks 2; dorsal anterior margin of A10 with 2 lobes. **Material:** G100.

Foodplants: Predominantly *Acacia pycnantha* Benth.; also recorded from *A. brachybotrya* Benth. and *Cassia ?nemophila* A. Cunn. (McFarland 1979).

Specimens examined: 113 ♂ 77 ♀. QUEENSLAND: Stanthorpe, iv. JH 1 ♂ SAM; Talwood, iv. WBB 1 specimen QM. NEW SOUTH WALES: 1 km NNW of Goolgowl, v. IFBC & MSU 1 ♀ ANIC; 10 km SE of Gol Gol, v. IFBC 1 ♂ 1 ♀ ANIC; Tea Tree Creek nr Armidale, v. CWF 1 ♂ ANIC. VICTORIA: Birchip, iv. 8 specimens NMV, iv. 1 ♂ SAM; Gippsland, 1 ♀ NMV; Gisborne, iv. 1 ♀ NMV, iv. GL 1 ♀ SAM; Hamilton, 1 ♀ NMV; Haeckirch, iv. LRK 1 specimen QM; Melbourne, 1 ♀ SAM; Springvale, v. 1 ♀ NMV. SOUTH AUSTRALIA: Adelaide, iv. v. JGOT 1 ♂ 1 ♀ SAM, v. 1 ♂ SAM, v. EA 3 ♀ SAM; Aldgate, v. 1 ♀ SAM; Athelstone, iv., v. JJIS 2 ♂ 2 ♀ SAM; Belair, iv. FMA 1 ♀ SAM; Blackwood, v. NBT 1 ♂ 1 ♀ ANIC, iii., iv., v. NMcf 2 ♂ 3 ♀ ANIC; ill., iv., v. NBT 20 ♂ 11 ♀ SAM, iv. VHM 1 ♀ SAM, iv. EA 1 ♀ SAM, v. EA 1 ♀ SAM, v. OBL 1 ♂ 5 ♀ SAM; Bowhill, iv. FMA 1 ♀ SAM; Burnside, 1 ♀ SAM; 100 km E of Ceduna, v. IFBC & MSU 2 ♂ ANIC; Glen Osmond, v. FMA 1 ♀ SAM; Highbate, iv. 1 ♂ SAM; Kadina, v. 1 ♀ PBMcQC; Lynton, iv., v. RHF 3 ♂ ANIC, iv. RHF 4 ♂ 4 ♀ SAM; Mambray Creek Nat. Pk., v. IFBC 1 ♀ ANIC; Monarto South, v. JWD 1 ♂ SAM; 48 km ESE of Morgan, v. IFBC & MSU 1 ♀ ANIC; Mt. Lofty, AMJ 1 ♀ SAM; Parkside, OBL 1 ♀ SAM, iv. FMA 1 ♂ SAM; Port Lincoln, 1 ♀ SAM; Renmark, v. PBMcQ 1 ♀ PBMcQC; Stonyfell, v. FMA 1 ♀ SAM; Waikerie, iv. 1 ♀ SAM; Warradale, iv., v. PBMcQ 4 ♂ 3 ♀ PBMcQC; 10 km SW of Wilmington, v. IFBC & MSU 1 ♂ ANIC; Whyalla, v. 1 ♀ NMV; 48 km S of Whyalla, v. IFBC 3 ♂ 3 ♀ ANIC. WESTERN AUSTRALIA: Brunswick

Inlet, 1 ♂ WAM; Buragup, 1 ♀ WAM; Cape Naturaliste, iv. IFBC & MSU 2 ♂ ANIC; Carlingup, v., 1 ♀ WAM; Claremont, 1 ♂ WAM; 26 km N of Collie, iv. IFBC & MSU 1 ♂ ANIC; 21 km WSW of Collie, iv. IFBC & MSU 2 ♂ ANIC; 27 km SE of Coolgardie, iv. IFBC & MSU 2 ♂ ANIC; Corrigin, 1 ♂ WAM; Crawley, vi. KRN 1 ♂ ANIC; Denmark, iii., iv. WBB 2 specimens QM; Drummond Cove 11 km N of Geraldton, v., vi. NMcf 5 ♂ ANIC; Dumbleyung 1 ♀ WAM; Dundas, 1 ♀ SAM; Hamel, v. 1 ♂ NMV; Katanning, v. KRN 1 ♀ ANIC; 1 ♂ ♀ WAM; Kojonup, iv., v., vi. ALR 8 ♂ 2 ♀ ANIC, iv., v. RJP 9 ♂ ANIC, iv., v. MMHW 6 ♂ ANIC, 1 ♀ SAM; Lake Grace, iv. 1 ♀ ANIC, iv. 3 specimens QM; 45 km W of Madura, iv. IFBC & MSU 2 ♂ ANIC; 29 km W of Mogumber, iv. IFBC & MSU 4 ♂ ANIC; 98 km E of Norseman, iv. IFBC & MSU 2 ♂ ANIC, 24 km N of Northampton, iv. IFBC & MSU 3 ♂ ANIC; 11 km S of Pemberton, iii. IFBC & MSU 1 ♂ 1 ♀ ANIC; Perth, v., viii. 1 ♂ 1 ♀ NMV; Pithara, iv. IFBC & MSU 1 ♂ ANIC, v. 1 ♀ WAM; Ravenswood, vi. FMA 3 ♂ 2 ♀ SAM; Stockyard Gully, Jurien Bay, vi. BE 1 ♀ WAM; Swan River, vii. 1 ♂ QM; Tammin, v., vi. 9 specimens NMV; Yanchep Nat. Pk., iv. IFBC & MSU 2 ♂ ANIC; Yuna, iv. IFBC & MSU 2 ♂ ANIC.

Distribution. see fig. 50, **Flight Period:** see fig. 18.

Comments: *T. angulosa* is widespread in dry sclerophyll forest and mallee areas in South and Western Australia extending to wet sclerophyll forest in southwestern Australia. However it is rare in this habitat further east. It is sympatric with *T. tetraclada* over a large part of its range. A favoured habitat is the open woodland of the Mt Lofty Ranges where *Acacia pycnantha* is commonly a dominant or co-dominant shrub. Adults emerge after a succession of cold nights in mid autumn and persist until late May.

Thalaina clara Walker

FIGS 7, 16, 18, 21, 31, 41, 50, 55.

Thalaina clara Walker 1855, p. 660; Meyrick Meyrick 1892, p. 654; Turner 1919, p. 388.

Holotype ♂ labelled "Australia 52-39" in BMNH.

Adult (fig. 55): Head with frons rounded, smoothly hair-scaled, whitish-buff; vertex roughly hair-scaled, rust colour; labial palpi with terminal segment and apex of second segment fuscous, remainder white; antenna of male laminate. Thorax white, anteriorly grey-white, orange at base of wings; legs with fore and mid femora and tibiae and all tarsi infuscated, hind femora and tibiae white; fore-

wing (fig. 7) with costa straight, gently arched apically, termen arched and slightly sinuate beneath apex, R_1 anastomosed with Sc and again with R_2 , ground colour shining white; narrowly black-margined red-brown streak from base to one-third costa then angled to mid-discal area where it bifurcates emitting one streak to tornus thence along posterior margin to near base and another streak tracing M_3 to mid termen then back to four-fifths costa, termen narrowly light fuscous, cilia orange posteriorly fuscous; hindwing shining white with a rounded fuscous subapical blotch never extending to anal angle, cilia white; forewing beneath white, costa and a triangular subapical blotch fuscous, costal edge of this blotch orange; hindwing beneath white, subapical blotch usually larger than on upperside and orange above M_1 ; wing expanse ♂ 38–48 mm, ♀ 40–48 mm, Abdomen white.

Male genitalia (fig. 21) with apex of gnathos with small spine; aedeagus (fig. 31) with cornuti of two compound spines one noticeably longer than other.

Female genitalia (fig. 41) with sclerotised section of ductus bursae longer than colliculum.

Final instar larva: Head capsule 3.2 mm wide, blue-green with small fuscous blotches on upper half; body bright olive green with four wavy whitish lines dorsally; enclosed green areas irregularly mottled with blue-green, extreme posterior margin of each segment whitish; fleshy yellowish lateral line irregularly edged with pinkish and fuscous below, lateral areas mottled with white and finely speckled black, two whitish subventral stripes on most segments and diagonally extended to thoracic legs and prolegs, ventral areas pale green with several whitish parallel lines; crochets 13–16 on A4, 15–19 on A5, 25–28 on A6 and 28–33 on anal claspers; length 33–37 mm, width 4.5–5.0 mm, Material: G128.

Pupa (fig. 16) dark brown in colour; cremaster hooks 6; dorsal anterior margin of A10 with 2 lobes. Material: G128.

Foodplant: *Aracia decurrens* (J. Wendl.) Willd.

Specimens examined: 117 ♂ 57 ♀. QUEENSLAND: Blackbutt, 1 ♀ UQ; Millmerran, v. JM 1 ♀ ANIC, v. 2 ♀ NMV, iv. JM 1 ♂ UQ; Toowoomba, iv. 2 ♂ 1 ♀ NMV, iii., iv., v., vii. EID 9 ♂ 4 ♀ UQ, v. JGM 1 ♀ UQ; NEW SOUTH WALES: Audley, v. HST 1 ♂ ANIC, Barrington House via Salisbury, v. GBM 1 ♀ UQ; Baryrene, iv. HST 1 ♀ ANIC; 8 km N of Bungwahl, iii.

IFBC & MSU 1 ♂ ANIC; Church Point, v. IFBC 1 ♀ ANIC; 7 km SW of Gosford, iii. IFBC & MSU 4 ♂ ANIC; Hornsby, iv. 2 ♂ 2 ♀ NMV; Killara, iv., v. 3 ♂ 1 ♀ NMV. Marulan, iv. 1 ♀ SAM; Millagong, iv. 2 ♂ 2 ♀ NMV; Mulgoa, LMR 1 ♂ ANIC; Narara, iv. LMR 4 ♂ 6 ♀ ANIC; National Park, iv. 1 ♂ NMV; Orange, ii. HST 1 ♂ 1 ♀ ANIC; Pine Creek via Cuff's Harbor, v. GBM 1 ♂ UQ; Roseville, iv. LMS 5 ♂ ANIC; 40 km S of Singleton, iii. IFBC 1 ♂ ANIC; Sydney, iv. 1 ♀ NMV; Toooloom Scrub, iii. EJD 2 ♂ ANIC; ii., iii. EJD 7 ♂ 1 ♀ UQ; Tubrahucra Creek, Barrington Tops, i. RS 1 ♂ ANIC, i. 1 ♂ NMV; 8 km S of Wauchope, iii. IFBC & MSU 1 ♂ ANIC; 15 km NE of Windsor, iii. IFBC & MSU 1 ♂ 1 ♀ ANIC. AUSTRALIAN CAPITAL TERRITORY: Black Mountain, ii., iii. IFBC 5 ♂ ANIC, iii. IFBC 1 ♂ UQ; Canberra, iv. IFBC 1 ♀ ANIC; Condor Creek 800 m, ii. IFBC 1 ♂ ANIC, 3 km N of Lee's Spring 1200 m, ii. IFBC & EDE 1 ♂ ANIC. VICTORIA: Balwyn, xi. 1 ♂ NMV; Betka River, Mallacoota, iii. 1 ♀ NMV; Canterbury, iv. 10 specimens NMV, v. 1 ♂ SAM; Castlemaine, iii. 1 ♂ NMV; Cheltenham, iv. 20 specimens NMV; Crib Point, iv. CCI 3 ♂ 2 ♀ ANIC; Dandenong, iv. 9 specimens NMV; Gisborne, iii., iv. GL 20 specimens NMV, iii., iv. GL 5 ♂ 1 ♀ SAM, iv. GL 1 ♂ UQ; Hazelwood, iv. JHC 1 ♂ ANIC; Macedon, xi., iii. 2 ♀ NMV; Melbourne. OBL 2 ♂ 1 ♀ SAM; Mitcham, iv. 5 ♂ 1 ♀ NMV; Moe, iii., iv. UCLG 1 ♂ 3 ♀ ANIC, iv. RW 2 ♂ ANIC, iv. GCLG 2 ♂ SAM, iv. 1 ♂ UQ; Mt Donna Buang, i. 1 ♂ NMV; Mt Erica, ii. 1 ♀ NMV; Mt Waverley, 1 ♂ NMV; Myrtleford, iv. 1 ♂ NMV; Oakleigh, 1 ♀ NMV; Otway Ranges, ii. PBMeQ 1 ♂ 1 ♀ PBMeQC; Sale, iv. 2 ♂ NMV; Springvale, iv., v. 6 specimens NMV, v. 1 ♂ SAM, iv. LBT 1 ♂ UQ; Tara Valley Natl Park, ii. PBMeQ 2 ♀ PBMeQC; Thurra River nr. Cape Everard, iii. 1 ♂ NMV; Traralgon, iv. 2 ♂ 2 ♀ NMV; Wakroanga, iv., 1 ♀ SAM; Wandlin, 2 ♂ NMV; Woori Yallock, iii. 1 ♂ NMV. TASMANIA: Mole Creek, iv. JRC 2 ♂ TMAG. SOUTH AUSTRALIA: Adelaide, OBL 2 ♂ SAM; Naracoorte, iii., iv. IOW 1 ♂ 3 ♂ ANIC, Woodville, ix. TB 1 ♂ SAM.

Distribution: see fig. 50. **Flight Period:** see fig. 18

Comments: *T. ultra* ranges over much of the same type of habitat as *T. selenaea*, however its presence in Tasmania and near Adelaide requires confirmation.

Thalaina inscripta Walker

FIGS 8, 18, 22, 32, 42, 50, 56.

Thalaina inscripta Walker 1855, p. 661; Meyrick 1892, p. 655; Lower 1893, p. 290 (larva); Turner 1919, p. 388.

Plusargyria principaria Herrich-Schäffer 1855, pl. 78, fig. 446.

Absyrtus principaria Herrich-Schäffer, Guenée 1857, p. 227.

Thalania hieroglyphica Lower 1893, p. 289, Goldfinch 1944, p. 191.

Types of inscripta: lectotype ♂ labelled "V.D.L. 51-153" in BMNH, hereby designated, 1 ♂ 1 ♀ paratype, 1 ♂ labelled "V.D.L. 54-9" in BMNH, hereby designated, 1 ♀ labelled as fur lectotype, in BMNH, hereby designated.

Type of principaria: not in Zoological Institute, Martin Luther University, Wittenberg, GDR (N. Gossler, pers. comm.).

Holotype ♂ of *hieroglyphica* labelled "April '93, 906 Blackwood = 906 *T. hieroglyphica* Lower" in SAM.

Adult (Fig. 56): Head with frons rounded, smoothly hair-scaled, whitish-buff; vertex with rough hair-scales, pale fuscous; labial palp with terminal segment and most of second segment pale fuscous, second segment beneath with long white scales; antenna of male laminate. Thorax grey-white becoming whiter posteriorly, pale fuscous at base of wings; forewing (fig. 8) with costa nearly straight, apex produced; termen strongly arched and sinuate beneath apex; R_1 anastomosed with Sc and again with R_{2+3} ; shining white, markings ochreous to pale fuscous, narrowly margined darker; streak from base to one-third costa, then extending to mid disc where it bifurcates into an upper arm reaching mid termen thence to costa at three-quarters, and a lower arm reaching to tornus, thence thickly along posterior margin to base, termen with small semi-circular markings at the extremities of M_{2+3} , CuA_1 , and CuA_2 and a larger triangular blotch below apex, cilia pale fuscous; hindwing shining white with a moderate fuscous subapical blotch sometimes extending to termen and costa; forewing beneath white with upper-side markings visible; costal half of these being faintly outlined with pale fuscous below; hindwing beneath white, subapical blotch reproduced and usually larger; wing expanse ♂ 38-44 mm, ♀ 40-42 mm. Abdomen white with pale fuscous shadings above.

Male genitalia (fig. 22) with tegumen rather narrow; aedeagus (fig. 32) with cornuti of two subequal compound spines.

Female genitalia (fig. 42) with papillae anales rather large; ductus bursae relatively short.

Final instar larva: (modified from Lower 1893), Length 26 mm. Head capsule 2.3 mm wide, pale green with small fuscous blotches

across upper frons; body green, lightly flecked darker, a mid dorsal stripe of dense blackish speckling; two fine dorsolateral whitish stripes; fleshy whitish lateral line irregularly blotched with fuscous above and below; a thin whitish subventral stripe; ventrally pale green with a white mid ventral stripe; erotchetts 13-14 on A4, 12 on A5, 25 on A6 and 28-29 on anal claspers. Material: One specimen "Tas., 15 km NNW of Buckland, 19 viii. 1980. On *Acacia mearnsii* De Wild, P. B. McQ.", in TDA.

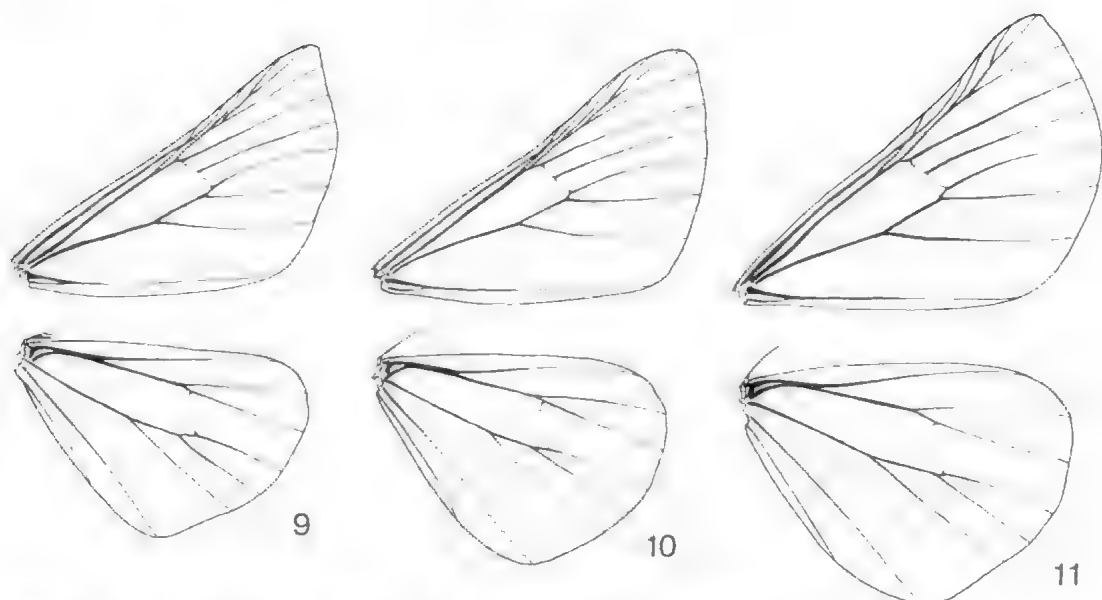
Pupa: mid brown in colour; 6 cremaster hooks; dorsal anterior margin of A10 with 2 lobes. Material: One specimen labelled as above, but "pupa 3 ix. 1980", in TDA.

Foodplants: *Acacia decurrens* (J. Wendl.) Willd., *A. mearnsii* De Wild.

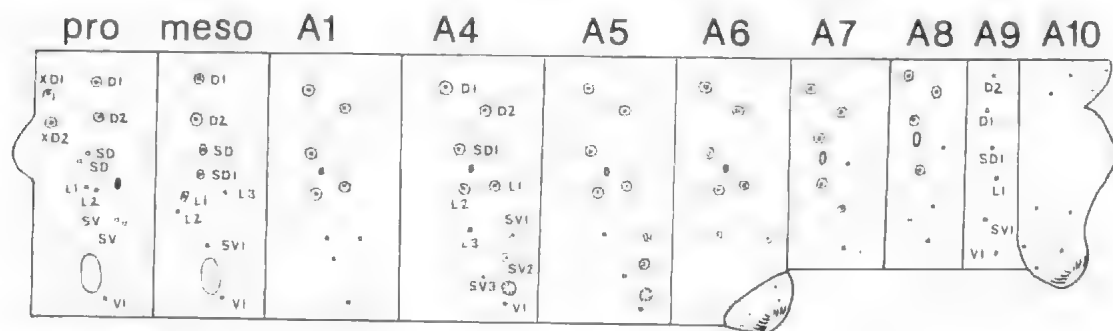
Specimens examined: 58 ♂ 21 ♀, QUEENSLAND: Yeppoon, i. IFBC 1 ♀ ANIC; NEW SOUTH WALES 1.6 km S of Mt Tinderry 1600 m, ii. IFBC & MSU 1 ♂ ANIC; 5 km SE of Pilot Hill, Bago Forest, Batlow, iii. TGC 1 ♂ ANIC; AUSTRALIAN CAPITAL TERRITORY: Blondell's Creek Rd. 1000 m iii. IFBC 1 ♂ ANIC; VICTORIA: Bendigo, iv. 1 ♀ NMV; Castlemaine, iv. 4 ♂ 1 ♀ NMV; Gippsland, iii., iv. 30 specimens NMV; Gisborne, iii., iv. 4 ♂ 2 ♀ SAM, iii., iv. 30 specimens NMV; Macedon, iii. 2 ♂ NMV; Melbourne, iv. 1 ♂ NMV; Toolangi, iv. 3 ♂ 1 ♀ NMV; Wandin, iv. 5 specimens NMV. TASMANIA: Bellerive, iii. BM 1 ♂ ANIC; Cressy, iv. 1 ♂ TDA; Fern Tree iii. RJH 1 ♂ TDA; Heiliger Gorge ii. IFBC & MSU 1 ♀ ANIC; Kingston iv. JRC 2 ♀ UQ, iv. JRC 2 ♂ ANIC, iv. JRC 2 ♂ 4 ♀ TMAQ; iv. JRC 1 ♂ NMV; L. Leake 1300 m, ii. IFBC & MSU 1 ♀ ANIC; 16 km W of Maydena, ii. 1 ♂ NMV; Mt Barrow 800 m, iii. IFBC & MSU 1 ♂ ANIC; Mt Field National Park 160 m, ii. IFBC & MSU 1 ♂ ANIC; Mt Nelson 200 m, iii., iv. PBMcQ 5 ♂ 3 ♀ TDA; Mt Wellington 270 m, i., ii., iii., iv., BM 15 ♂ 5 ♀ ANIC; Ouse, iii., iv. 3 ♂ TDA; Pyengana 310 m, iii. IFBC & MSU 2 ♂ 1 ♀ ANIC; Ridgeway, ii. 1 ♂ NMV; Travallyn, iii. RJH 1 ♂ TDA; 21 km S of Westbury iii. IFBC & MSU 1 ♂ ANIC.

Distribution: see fig. 50. *Flight Period*: see fig. 18.

Comments: *T. inscripta* is an interesting species with larvae adapted in colour pattern to living on bipinnate *Acacia* food plants. It is the most cold-tolerant of the genus, being the commonest species over much of Tasmania where it occurs in open woodland up to 1000 m; it also occurs in the Australian Alps up to 1500 m. The single record from central Queensland is noteworthy in view of the ab-



Figs 9-11. Venation of *Thalaina* spp. 9. *T. paronycha*; 10. *T. allochroa*; 11. *T. kimba*.



12

Fig. 12. Setal map of final instar *Thalaina clara*.

sence of records from northern N.S.W. and southern Queensland.

Adult moths were abundant in an open eucalypt woodland in which *Acacia mearnsii* was the dominant tall shrub about 8 km south of Steppes, central Tasmania, on 6 iii. 1980. In the mid-afternoon sunshine months were resting on the undersides of *Acacia* leaves sometimes two or three per tree, and were readily put to flight by walking near them. Their flight was extremely erratic and sustained; and generally less than 5 m above the ground. Although conspicuous in flight, they were not easy to see at rest on the trees in the dappled light when looking against the sky.

Thalaina chionoptila (Turner) comb. nov.

FIGS 5, 18, 23, 33, 43, 49, 57.

Macqueenia chionoptila Turner 1947, p. 102.

Types: lectotype ♂ labelled "Milmerran, Q. 25 APR. 1936 J. Macqueen : *Macqueenia chionoptila* Turn. TYPE" in ANIC, hereby designated; 4 ♂ 4 ♀ *paralectotypes*, 1 ♂, 3 ♀ "Milmerran, Q. 14-5-31 J. Macqueen", 1 ♂ "Milmerran, Q. 27-4-31 J. Macqueen", 1 ♂ Milmerran, Qld. 27 APR. 1935 J. Macqueen", 1 ♂ Milmerran, Qld. 8 May 1935 J. Macqueen", 1 ♀ "Milmerran, Q. 20-4-31 J. Macqueen : Genitalia M818 P.B. McQ. 1978" in ANIC, hereby designated.

Adult (fig. 57): Head with frons rounded, smoothly scaled, whitish buff; vertex with erect hair-scales, bright red-brown; labial palp buff, becoming whitish towards base of second segment; antenna of male strongly bipectinate.

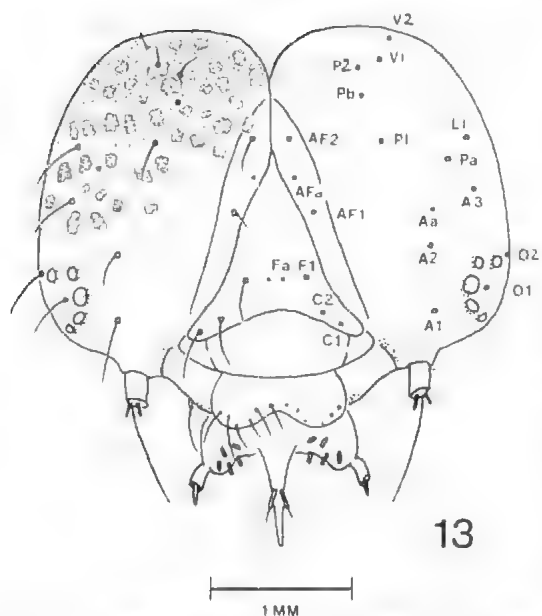
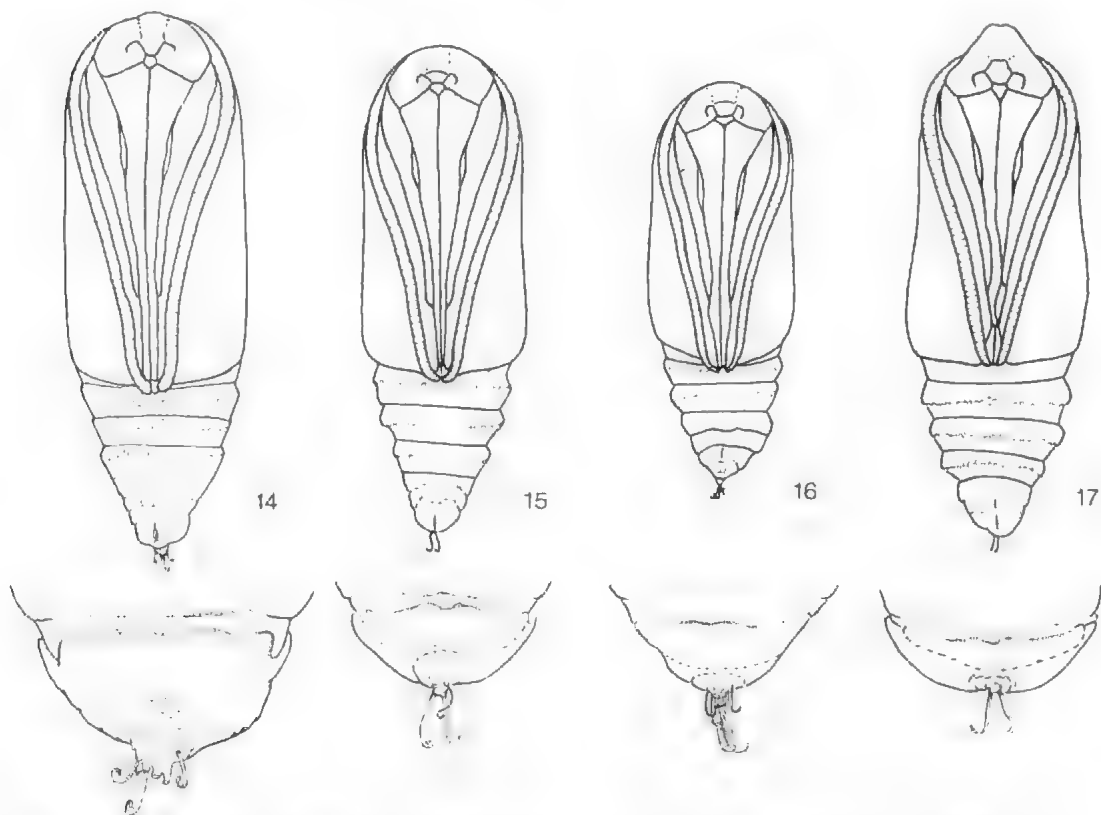


Fig. 13. Head capsule of final instar *Thalaina angulosa*.

Thorax greyish-white on anterior third, remainder white; legs white with exterior of fore and mid legs infuscated; forewing (fig. 5) with costa straight, apex pointed, termen slightly sinuate beneath apex and hardly arched, R_1 often connected with Sc by short bar and sometimes anastomosed with R_2 ; ground colour above shining white, orange-brown spot at base of costa, extreme costal, termen and posterior margins orange-brown, cilia orange-brown; hindwing shining white; subapical and subtoral fuscous spot present, cilia white; forewing beneath furtively infuscated; orange costal streak from near base to five-sixths, inner margin streak absent; hindwing beneath white, fuscous spots as above but larger; wing expanse ♂ 48–52 mm, ♀ 52–54 mm.

Male genitalia (fig. 23) with socii rather pendulous, apex of gnathos enlarged with numerous small spines surmounted by a larger single spine, furca relatively short with prongs of unequal length; aedeagus (fig. 33) with cornuti of two groups of small spines.



Figs 14–17. Pupa and cremaster of *Thalaina* spp. 14. *T. selenaca*; 15. *T. angulosa*; 16. *T. clara*; 17. *T. macfarlandi*.

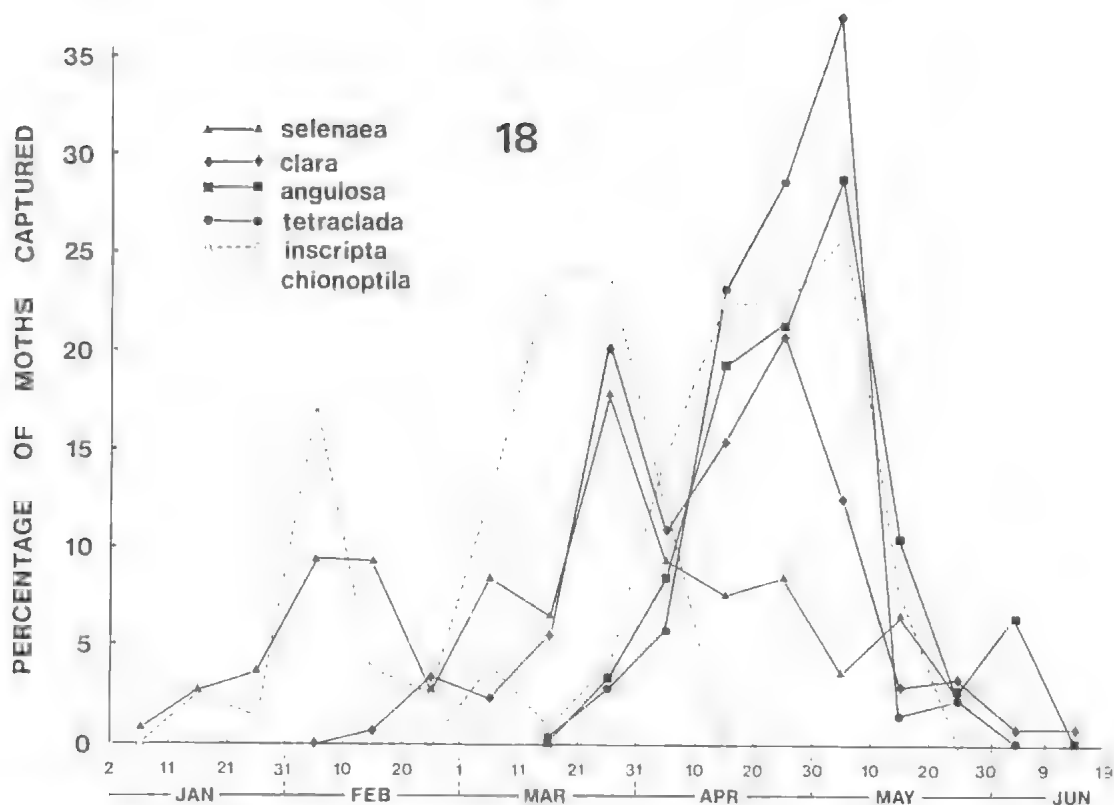


Fig. 18. Flight period of adults of some *Thalaina* spp.

Female genitalia (fig. 43) with colliculum rather broad.

Immature stages not recorded except that larva pupates underground.

Foodplant: *Acacia harpophylla* Benth.

Specimens examined: QUEENSLAND: Millmerran, iv., v. JM 5 ♂ 4 ♀, ANIC; Millmerran, iii., iv., v. JM 28 specimens, NMV; Millmerran, iv., v. JM 8 specimens, QM; Millmerran, iii., iv., v. JM 4 ♂ 8 ♀, SAM; Millmerran, iii., iv., v. JM 5 ♂ 4 ♀, UQ. NEW SOUTH WALES: Trangie, iv. RL 1 ♂, ANIC.

Distribution: see fig. 49. *Flight period*: see fig. 18.

Comments: *T. chionoptila* is mainly known from a long series of adults taken at Millmerran in the 1930's and 40's by J. Macquoen. Land clearing since then has much reduced the availability of its foodplant in southern Queensland. On present evidence it is the most localised member of the genus.

Thalaina tetracлада (Lower) comb. nov.

FIGS 1, 18, 24, 34, 44, 51, 58.

Amelora tetracлада Lower 1900, p. 406.

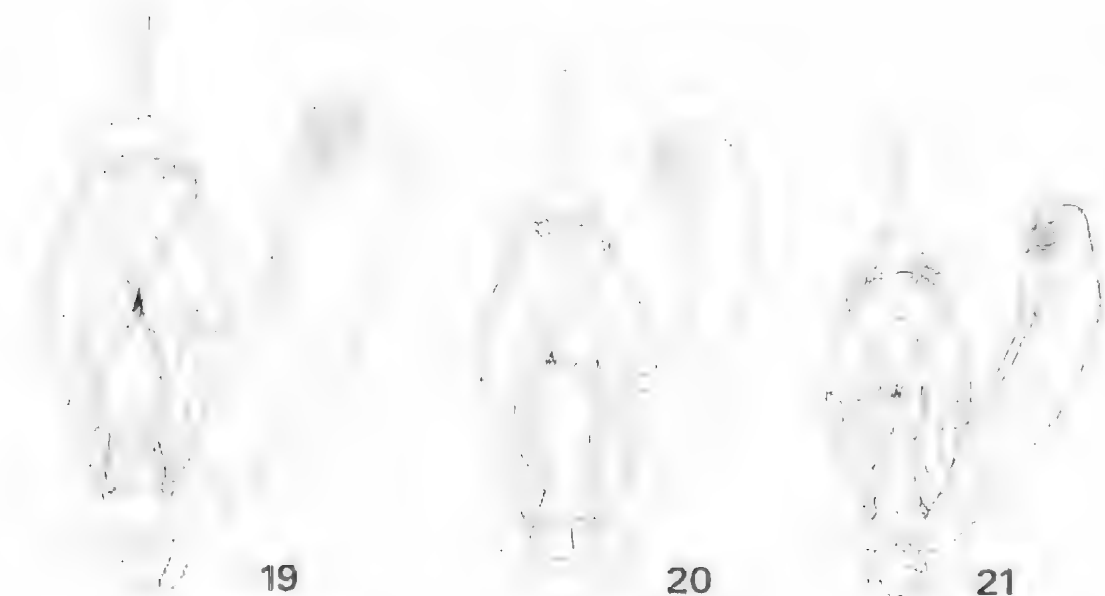
Thalainodes tetracлада Lower 1902, p. 231; Turner 1919, p. 386; Wilson 1972, p. 123.

Thalainodes nessostoma Turner 1919, p. 386; Wilson 1972, p. 123. syn. nov.

Holotype ♂ of *tetracлада* labelled "3459 TYPE Broken Hill 6.5.1899 : *tetracлада* Low. 3459", in Lower's hand, in SAM.

Holotype ♀ of *nessostoma* labelled "probably Bourke coll. Helms : *Thalainodes nessostoma* Turn. TYPE : G. M. Goldfinch Collection" in AM.

Adult (fig. 58): Head with frons naked and bearing rounded projection (fig. 1); vertex orange or tan; labial palp pale brown above, white below; antenna of male strongly bipectinate. Thorax orange or tan above with inner margin of tegulae and sides of thorax white; legs white, exterior of fore and mid femur and tibia and all tarsi infuscated; forewing with costa nearly straight, apex produced, termen gently arched and oblique, ground colour above shining white, orange or tan costal streak from apex to one-half costa attenuated anteriorly then continued as fine streak to base; faintly black-margined orange or tan streak



Figs 19–21. Male genitalia. 19. *T. selenacea*; 20. *T. angulosa*; 21. *T. clara*. Scale lines 1 mm.

from base to just above mid termen tracing M_3 and emitting similar streak from about one-fifth to one-third tracing CuA_2 to termen; streak along posterior margin from near base to tornus, termen narrowly orange or tan, cilia orange or yellow; hindwing shining white; large fuscous subapical blotch, projection of which often touches termen or is continued subterminally to anal angle, cilia white; forewing below white, lightly infuscated basally and below CuA_2 , costa and termen narrowly orange or tan; fuscous subapical blotch posteriorly orange or tan; hindwing below shining white; maculation as above; wing expanse ♂ 38–48 mm, ♀ 38–46 mm.

Male genitalia (fig. 24) with uncus rather long, gnathos with a large apical spine bearing numerous smaller ones, furca rather linear and both forks of equal length; aedeagus (fig. 34) curved basally, cornuti of two groups of about 3 spines.

Female genitalia (fig. 44) with apophyses anteriores rather short, colliculum longer than sclerotised band of ductus bursae.

Specimens examined: 37 ♂ 33 ♀ NEW SOUTH WALES: Broken Hill, v. OBL 2 ♂ SAM; Bourke, 1 ♀ AM; SOUTH AUSTRALIA: 10 km SW of Iron Knob, v. IFBC 4 ♂ 10 ♀ ANIC; 64 km E of Nullabor, iii. IFBC & MSU 1 ♂ ANIC; 89 km E of Nullabor, v. IFBC & MSU 1 ♂, 1 ♀ ANIC;

46 km SW of Whyalla, v. IFBC 4 ♀ ANIC; Whyalla, v. 2 ♀ NMV; WESTERN AUSTRALIA: 27 km SE of Coolgardie, iv. IFBC & MSU 3 ♂ 2 ♀ ANIC; Dalwallinu, iv. LEK 1 specimen WAM; Dumbleyung, iv. HU 2 specimens WAM; Kalbarri Nil Park, iv. IFBC & MSU 2 ♂ ANIC; Kojonup, iii. RJP 1 ♂, iii. RB 1 ♂, iv. ALR 5 ♂, iv. RJP 6 ♂ 2 ♀, iv. MMHW 3 ♂ 1 ♀, v. RJP 1 ♂, v. ALR 1 ♂, v. MMHW 1 ♂, all ANIC; 45 km W of Madura, iv. IFBC & MSU 2 ♀ ANIC; Merredin, LJN 1 specimen QM; 46 km W of Merredin, iv. IFBC & MSU 1 ♂ ANIC; 29 km W of Mogumber, iv. IFBC & MSU 1 ♀ ANIC; 97 km E of Norseman, iv. IFBC & MSU 1 ♀ ANIC; 24 km N of Northampton, iv. IFBC & MSU 3 ♂ 1 ♀ ANIC; Pithara, iv. IFBC & MSU 1 ♂ 4 ♀ ANIC; Tammin, v. 2 ♀ NMV.

Distribution: see fig. 51. **Flight period:** see fig 18.

Comments: This species ranges widely across the subinterior of southern Australia, reaching the coast along the Nullabor Plain and south-west Australia. East of W.A. its range lies between the 20 cm and 35 cm isohyets whereas in southwestern Australia it extends to the 100 cm isohyet, apparently occupying the niche filled by the three forest species in south-eastern Australia. Some clinal variation exists; specimens from the central and eastern parts of its range are usually smaller (mean wing expanse 40 mm) and the forewing markings



Figs 22–24. Male genitalia. 22, *T. inscripta*; 23, *T. chionoptila*; 24, *T. tetraclada*.

are tan or ochreous-orange, whereas in S.W. Australia they are usually larger (mean wing expanse 46 mm) and with bright orange markings. There are no genital differences between extremes of the cline.

Thalaina macfarlandi (Wilson) comb. nov.

FIGS 2, 17, 25, 35, 45, 51, 59.

Thalainodes macfarlandi Wilson 1972, p. 123.

Types: holotype ♀ labelled "NTHN. TERR., 148 km S of Alice Springs 26 April 1966 N. McFarland at uv light" in SAM; allotype and paratypes, see Wilson (1972).

Adult (figs 2, 59) adequately described by Wilson (1972); wing expanse ♂ 38–44 mm, ♀ 38–50 mm.

Male genitalia (fig. 25) with tegumen and valva elongate, apex of gnathos with large recurved spine bearing some smaller ones, furca goblet-shaped, juxta elongate; aedeagus (fig. 35) with apex produced, cornutus a sclerotised plate bearing small marginal spines.

Female genitalia (fig. 45) with very long ductus bursae and without sclerotisation.

Egg ovoid, pale green with an elongated brown blotch, 1.0 mm long x 0.8 mm wide. Material: G180.

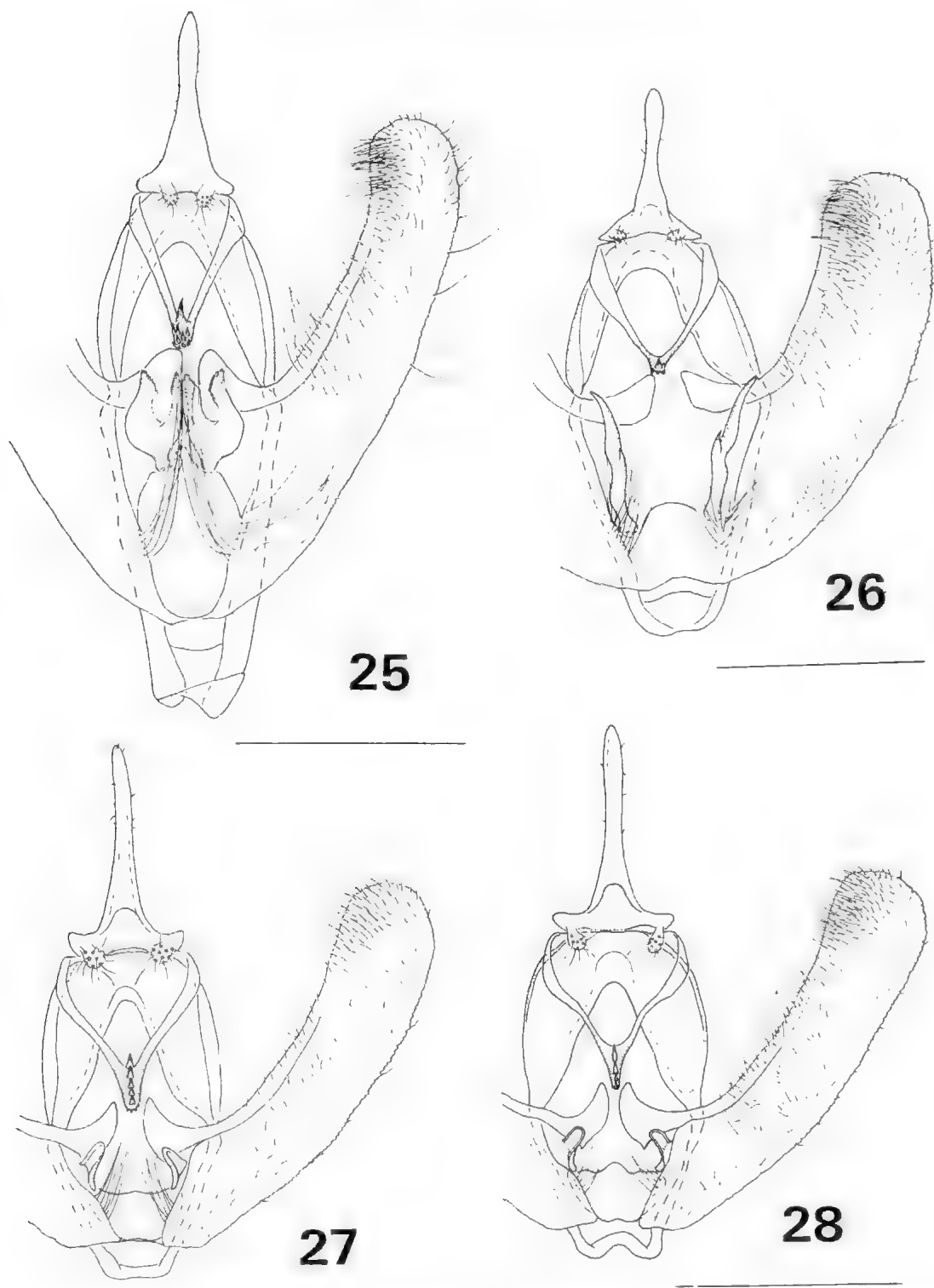
Final instar larva: Head capsule 3.3–3.4 mm wide, pale green with white band across vertex bearing many small fuscous blotches; body dull green, white lateral stripe strongly developed on pro- and mesothorax and again on A6 to

A9 but usually poorly developed or absent on intermediate segments, spiracles black and placed above this line. L setae on A2 to A7 arising in black blotches on lower margin of lateral stripe, anal claspers with two black anterior vertical stripes, ventral areas pale green with two whitish subventral stripes on A7 and A8 only; crotchets 13–14 on A4, 14–15 on A5, 28–30 on A6 and 45–48 on anal claspers, those on hind claspers tending to be biordinal; length 27–31 mm, width 5.0 mm. Material: G180.

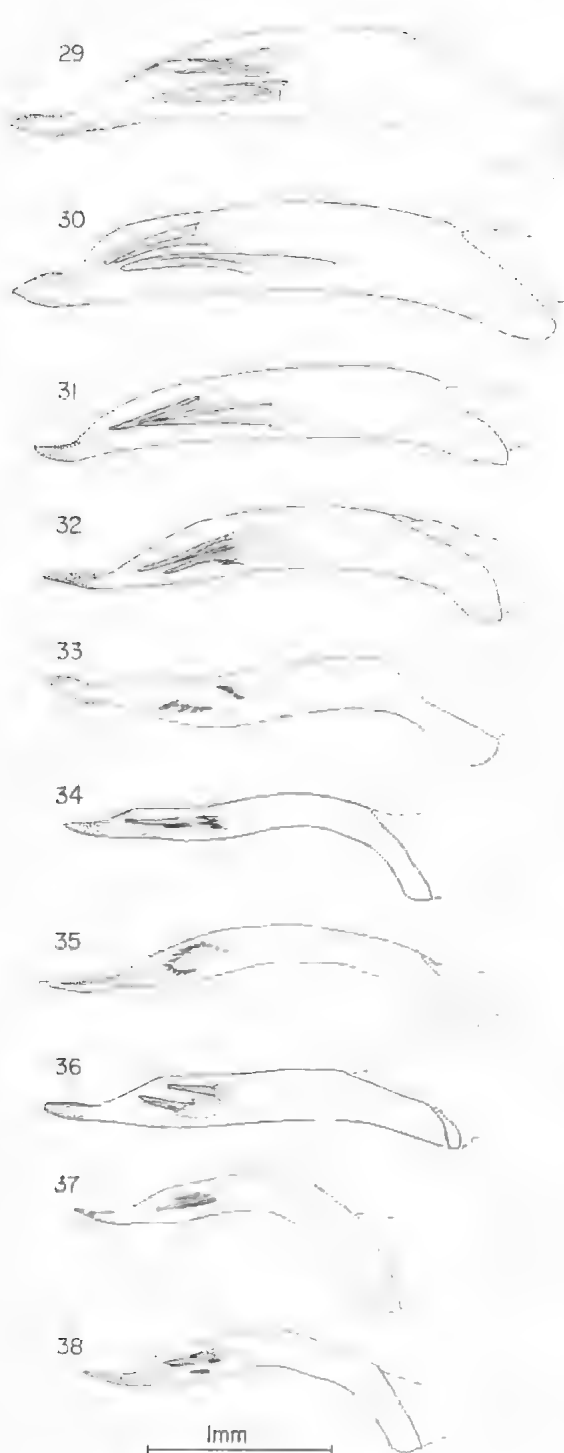
Pupa (fig 17) pale orange-brown; cremaster hooks 2; dorsal anterior margin of A10 with 2 lobes; length 11 mm, width 4.5 mm. Material: G180.

Foodplants: Unknown, but larvae thrive on *Acacia pycnantha* as a surrogate host (McFarland 1979).

Specimens examined: 14 ♂ 16 ♀. QUEENSLAND: Cunnamulla, v. NG 1 ♂ AM; 24 km S of Millmerran, iv. IFBC 1 ♀ ANIC. NEW SOUTH WALES: 30.50S 146.33E 23 km SSE of Byrock, v. EDE & MSU 1 ♂ 2 ♀ ANIC; Cobarr, iv. v. VJR 2 ♀ ANIC; 29 km E of Vaughan Springs HS, vi. KJMcK 1 ♀ ANIC. SOUTH AUSTRALIA: 27.18S 133.25E Ammaroodinna Creek, v. PBMcQ 1 ♂ PBMcQC; 160 km NNW of Coober Pedy nr Wintinna, v. NMcf & TN 1 ♂ SAM; 61 km S of Kulgera, v. NMcf & TN 1 ♂ SAM, NORTHERN TERRITORY: 19 km E of Alice Springs, v. NMcf & TN 3 ♂ ANIC; 1 ♂ 1 ♀ AM, 1 ♀ BMNH, 1 ♂ 1 ♀ NMIV; 45 km WSW of Alice Springs, v. NMcf & TN 1 ♀ SAM; 148 km S of Alice Springs, iv. NMcf



Figs 25–28. Male genitalia. 25. *T. macfarlandi*; 26. *T. kimba*; 27. *T. paronycha*; 28. *T. allochroa*. Scale lines 1 mm.



Figs 29–38. Aedeagi of *Thalaina* spp. 29. *T. selena*; 30. *T. angulosa*; 31. *T. clara*; 32. *T. inscripta*; 33. *T. chionoptila*; 34. *T. tetraclada*; 35. *T. macfarlandi*; 36. *T. kimba*; 37. *T. paronycha*; 38. *T. allochroa*.

1 ♀ SAM; 24.20S 131.35E Amadeus Basin nr Reedy Rockhole, vi. PR 4 ♀ ANIC; 23.48S 132.21E 5 km NE of Gosse's Bluff, v. HP 4 ♂ 1 ♀ ANIC.

Distribution: see fig. 51. *Flight Period*: late April to early June.

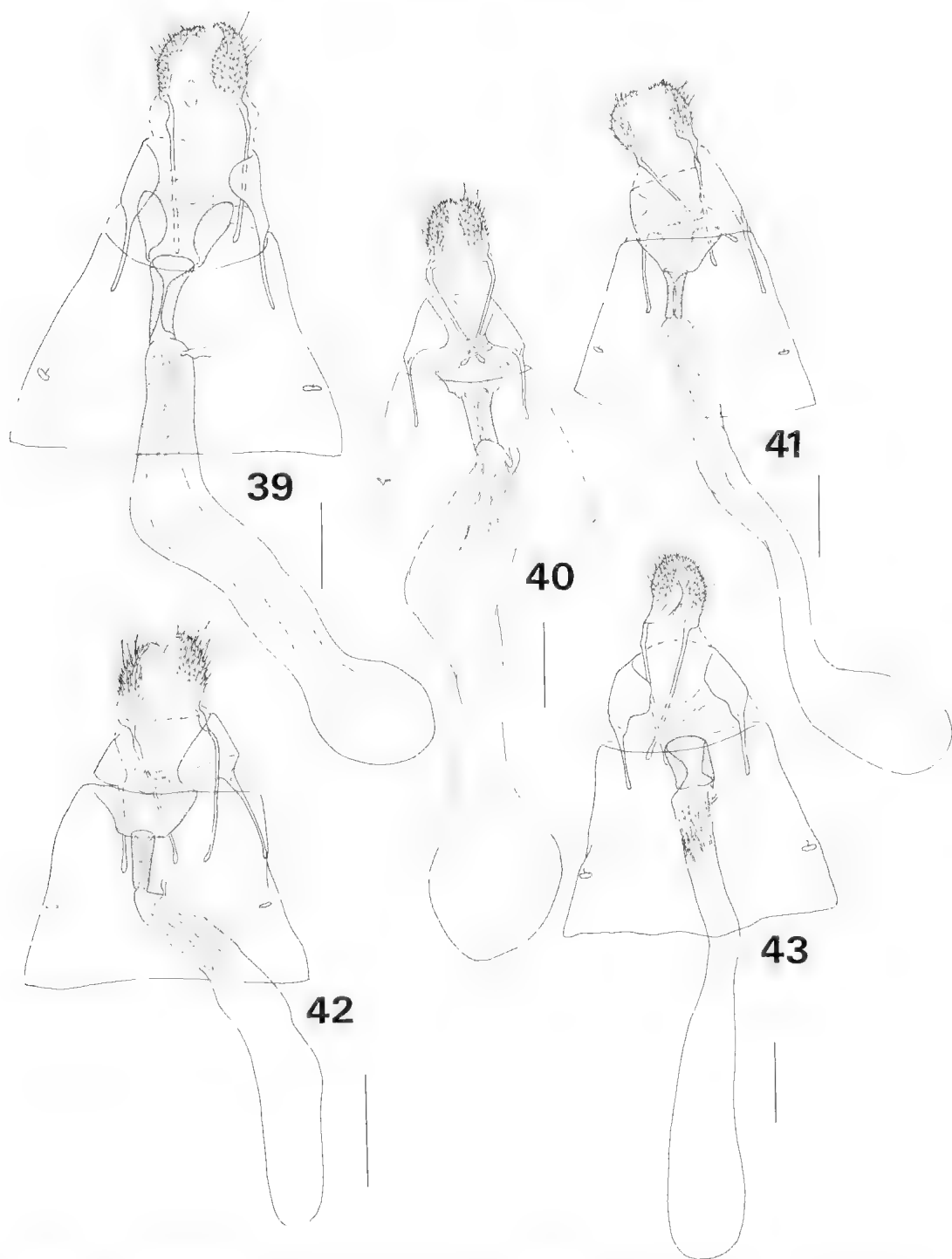
Comments: The dispersed nature of the few locality records for *T. macfarlandi* suggests a wide distribution in central Australia.

***Thalaina kimba* sp. nov.**

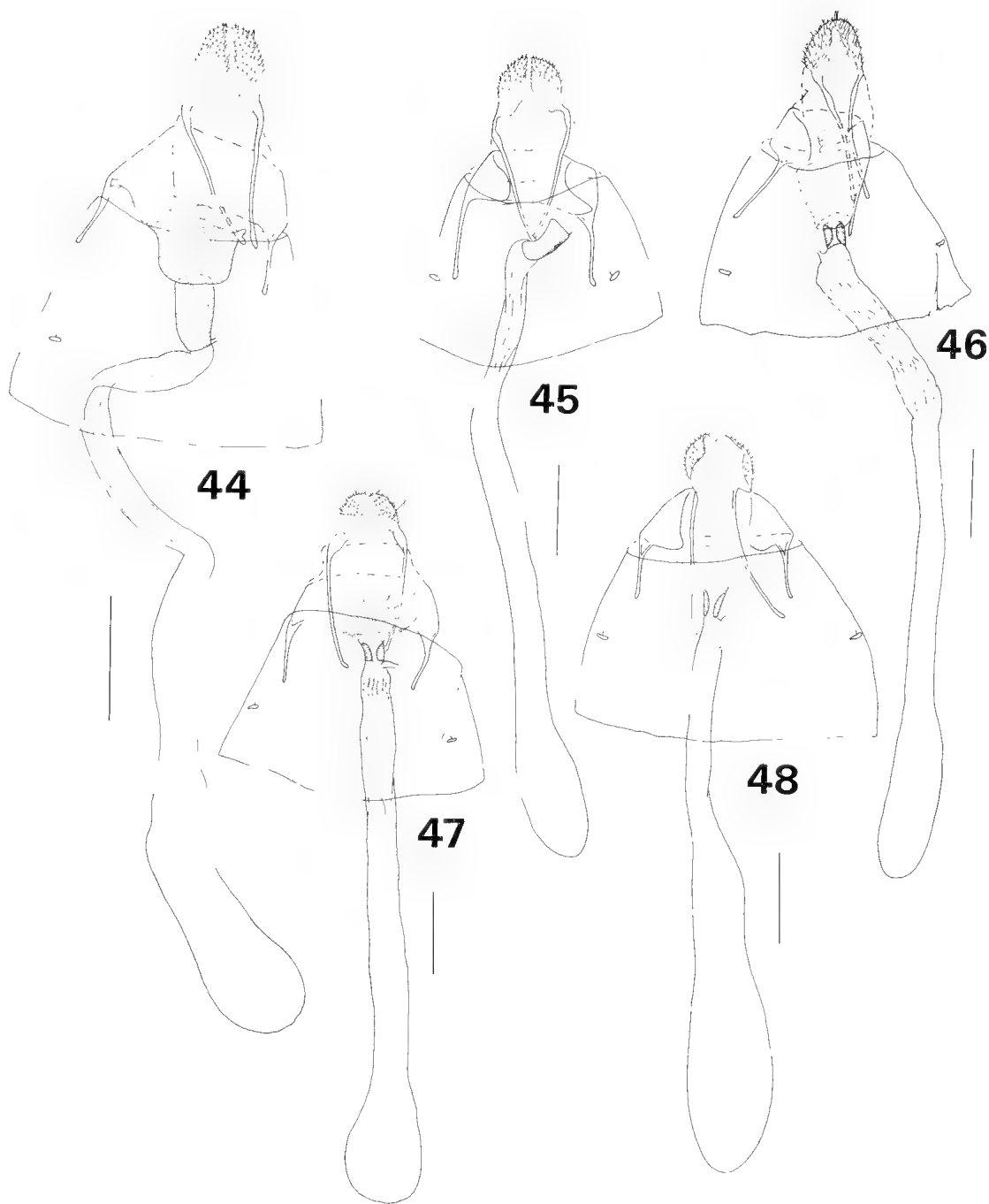
FIGS 11, 26, 36, 46, 51, 62, 63

Types: holotype ♂ labelled "32.51S 141.37E 100 km S by E of Broken Hill, N.S.W. 3 May 1976 I.F.B. Common E. D. Edwards: genitalia slide M846 PBMcQ 1978" in ANIC; 10 ♂ 8 ♀ paratypes, 2 ♂ same data as holotype, in ANIC; 1 ♂ labelled "6 miles S.W. of Iron Knob, S.A. 7 May 1970 I.F.B. Common: genitalia slide M842 PBMcQ 1978" in ANIC; 1 ♂ labelled "6 miles SE of Gol Gol, N.S.W. 5 May 1970 I.F.B. Common" in ANIC; 1 ♂ labelled "100 km SE of Broken Hill, N.S.W. 29 April 1976 I.F.B. Common E. D. Edwards" in ANIC; 1 ♂ labelled "1 km NNW of Goolgowi, N.S.W. 5 May 1976 I.F.B. Common E. D. Edwards" in NMV; 1 ♂ same data as for previous specimen in SAM; 2 ♂ same data as for previous specimen in ANIC; 1 ♂ 1 ♀ labelled "33.23S 141.40E 82 km NW of Wentworth, N.S.W. 28 April 1976. I.F.B. Common E. D. Edwards" in BMNH; 1 ♀ labelled "31.49S 141.12E Umberumberka Reserve, 9 km NNW of Silverton, N.S.W. 1 May 1976 I.F.B. Common E. D. Edwards" in ANIC; 1 ♀ labelled "30.50S 146.33E 23 km SSE of Byrock, N.S.W. 8 May 1973 E. D. Edwards & M. S. Upton: genitalia slide M845 PBMcQ 1978" in ANIC; 1 ♀ labelled "Mambray Creek Nat. Park, S.A. 11 May 1970 I.F.B. Common: genitalia slide M843 PBMcQ 1978" in ANIC; 1 ♀ labelled "30 miles SW of Whyalla, S.A. 9 May 1970 I.F.B. Common: genitalia slide M822" in ANIC; 1 ♀ labelled "Kimba 12.5.1963 R. E. Harris" in SAM; 1 ♀ labelled "Minnipa, S.A. May 1970" in PBMcQ; 1 ♀ labelled "Moorunde Wombat Reserve, nr. Blanchetown, S.A. 12 May 1974 P. B. McQuillan" in PBMcQC.

Adult (Figs 62, 63): Head with frons naked, bearing long rectangular projection emarginate at apex; vertex of head rough-scaled, greyish with suggestion of fuscous transverse bar behind antennae; labial palpi with terminal segment white; antenna in male shortly bipectinate. Thorax with anterior and posterior thirds fuscous-grey, mid-third and tegulae pale grey; legs infuscated, except hind femur and tibia; forewing (fig. 11) with costa straight in male, slightly recurved in female, termen sinuate beneath apex and strongly arched, R_1



Figs 39–43. Female genitalia. 39. *T. selenaea*; 40. *T. angulosa*; 41. *T. clara*; 42. *T. inscripta*; 43. *T. chionoptila*. Scale lines 1 mm.



Figs 44–48. Female genitalia. 44. *T. tetraclada*; 45. *T. macfarlandi*; 46. *T. kimba*; 47. *T. paronycha*; 48. *T. allochroa*. Scale lines 1 mm.

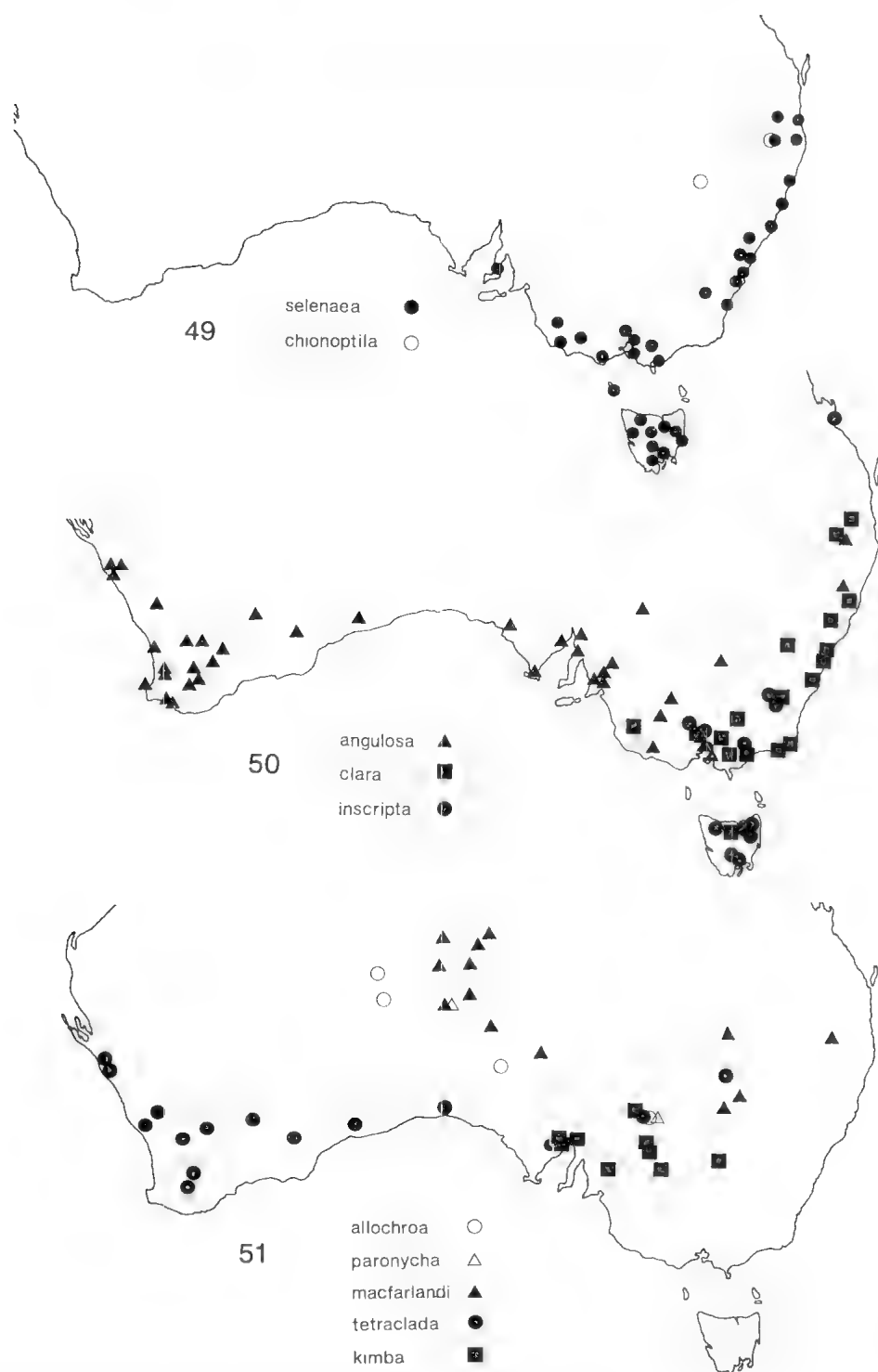


Fig. 49. Distribution of *Thalaina selenaea* and *T. chionoptila*.

Fig. 50. Distribution of *Thalaina angulosa*, *T. clara* and *T. inscripta*.

Fig. 51. Distribution of *Thalaina allochroa*, *T. paronycha*, *T. macfarlandi*, *T. tetraclada* and *T. kimba*.

anastomosed with Sc, ground colour white, markings suffused grey and sprinkled with bluish-white scales, base of costa blackish; very broad black-margined streak from one-third costa dilated posteriorly to mid disc where it bifurcates, one arm to mid termen thence angled to four-fifths costa and extending to half costa, other arm to tornus thence along posterior margin to near base where it is mixed with black; broad indented streak along termen, cilia brownish-grey becoming grey below M_3 ; hindwing translucent white with several irregular terminal and subterminal fuscous blotches; forewing beneath white with streak along posterior margin absent, discal streaks narrower and more sharply defined with fuscous, termen streak as above; hindwing beneath white, a subapical and a subterminal blotch only; wing expanse ♂ 38–44 mm, ♀ 40–44 mm.

Male genitalia (fig. 26) with valva rather broad, apex of gnathos with 3 or 4 small spines, furca long and sinuate with one branch poorly developed; aedeagus (fig. 36) with cornuti of single stout spine and group of 3 or 4 spines.

Female genitalia (fig. 46) with colliculum square, sterigma well developed, ductus bursae very long its proximal third with thick folds, remainder thinly membranous.

Distribution: see fig. 51. Probably widespread in mallee habitats from Eyre Peninsula through the Murray Mallee to western New South Wales.

Flight period: late April to early May.

Thalaina paronycha (Lower) comb. nov.

FIGS 9, 27, 37, 47, 51, 61.

Amelora paronycha Lower 1900, p. 407.

Thalainodes paronycha Lower 1902, p. 231;

Turner 1919, p. 386; Wilson 1972, p. 123.

Holotype ♀ labelled "3460 TYPE Broken Hill 24.5.98" in Lower's hand, in SAM.

Adult (fig. 61): Head with frons naked, bearing moderate truncate projection with longitudinal rib beneath; vertex with ochreous hair-scales which extend almost to extremity of frontal projection; labial palpi whitish; antenna of male strongly bipectinate. Thorax ochreous above, whitish below; legs tinged ochreous, fore-tibia very short, bearing apical spine; forewing (fig. 9) with costa straight, apex pointed, termen moderately arched, R_1 anastomosed with Sc, ground colour shining white, markings

dark ochreous or tan finely edged with brown, extreme costal edge white slightly broader from one-sixth to one-half costa; costal streak from base to apex narrowly continued along termen and slightly extended but broader along posterior margin; streak from one-quarter costa to termen above middle tracing M_3 , thence angled on termen to costa at three-quarters; diagonal streak from half discal streak to just above tornus, cilia ochreous; hindwing shining white tinged ochreous, pale fuscous subapical spot, cilia white; forewing beneath white, tinged ochreous on basal half and on margins, pale fuscous diagonal subapical spot; hindwing beneath white, subapical spot slightly larger and darker than above, small faint fuscous spot near termen between CuA_2 and A_1 ; wing expanse ♂ 36–40 mm, ♀ 42–44 mm. Abdomen ochreous.

Male genitalia (fig. 27) with tegumen broad, apex of gnathos elongate and bearing longitudinal row of about 6 stout spines, valva relatively long, furca reduced to small lobe; aedeagus (fig. 37) strongly curved, cornuti of single spine and another group of fused spines.

Female genitalia (fig. 47) with apophyses anteriores rather short, a band of sclerotisation at top of ductus bursae similar in length to colliculum, ductus bursae very long.

Specimens examined: 11 ♂ 26 ♀, NEW SOUTH WALES: Broken Hill, iv., v. OBL 10 ♂ 26 ♀ SAM, 11 specimens NMV; SOUTH AUSTRALIA: Ammatoodinna Creek 27.18S 133.25E, v. PBMcQ 1 ♂ 1 PBMcQC.

Distribution: see fig. 51. *Flight period*: mid April to late May.

Comments: This and the next species are rather isolated from the rest of the genus by structural features such as genitalia, presence of a spine on the fore tibia and the form of the frontal process.

Thalaina allochroa (Lower) comb. nov.

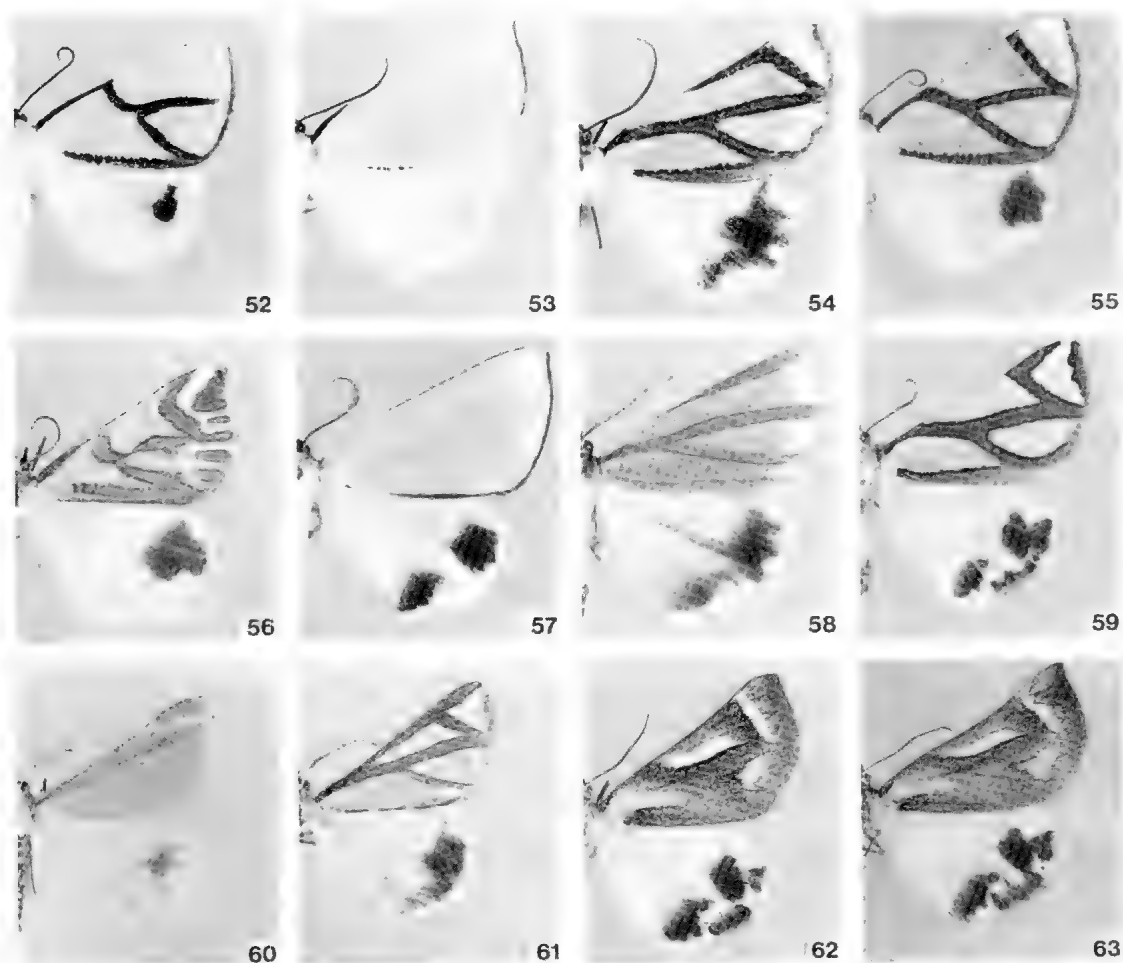
FIGS 10, 28, 38, 48, 51, 60.

Thalainodes allochroa Lower 1902, p. 232;

Turner 1919, p. 387; Wilson 1972, p. 123.

Holotype labelled "3.5.02 Broken Hill : 3779 : *Amelora allochroa* Lower TYPE" in Lower's hand, in SAM.

Adult (fig. 60) with head as for *T. paronycha*; vertex with ochreous-buff hair-scales which extend onto frontal projection; labial palpi white;



Figs 52–63. Adults of *Thalaina* spp. 52. *T. selenaea* ♂; 53. *T. selenaea* var. *punctilinea* ♂; 54. *T. angulosa* ♂; 55. *T. clara* ♂; 56. *T. inscripta* ♂; 57. *T. chionoptila* ♂; 58. *T. tetracлада* ♂; 59. *T. macfarlandi* ♂; 60. *T. allochroa* ♂; 61. *T. paronycha* ♂; 62. *T. kimba* holotype ♂; 63. *T. kimba* para-type ♀.

antenna of male strongly bipectinate. Thorax ochreous-buff above, whitish below; legs tinged ochreous; fore tibia very short, bearing apical spine; forewing (fig. 10) with costa straight, apex round-pointed, termen moderately arched, R_1 anastomosed with Sc, uniformly ochreous-buff, often sparsely flecked with black scales, extreme costal edge white especially between one-sixth costa and one-half, cilia ochreous; hindwing white, slightly ochreous tinged, pale fuscous subapical blotch emitting faint subterminal line to tornus, cilia white; forewing beneath whitish tinged with pale fuscous towards apex and costa; pale fuscous diagonal subapical spot; hindwing beneath white, subapical blotch slightly darker than above; wing expanse ♂ 36–44 mm. Abdomen ochreous.

Male genitalia (figs 28, 38) similar to *T. paronycha*, but apex of gnathos usually with 4 spines.

Female genitalia (fig. 48) almost indistinguishable from *T. paronycha*.

Specimens examined: 5 ♂ 2 ♀. NEW SOUTH WALES: Broken Hill, v. OBL 1 ♂ 1 ♀ NMV, v. OBL 6 ♀ SAM; Mootwingee Historical Site 31.14S 142.18E, v. IFBC & EDE 2 ♀ ANIC. SOUTH AUSTRALIA: Ammaroodinna Creek 27.18S 133.25E, v. PBMcQ 1 ♂ PBMcQC; McDouall Park, v. FWJ 1 ♀ SAM; Tallaringa Well, v. PA 1 ♀ SAM; 107 km S of Coober Pedy, v. NMcf 1 ♀ SAM. WESTERN AUSTRALIA: Giles, v. 2 ♂ PBMcQC; Skirmish Hill, 1 ♂ SAM.

Distribution: see fig. 51. *Flight Period*: May.

Comments: *T. allochroa* exhibits a radical departure from the basic colouration of the

genus but structurally it is virtually indistinguishable from *paronychia*. It is just possible that *allochroa* is only a Mendelian segregate of *paronychia* but breeding experiments are needed to confirm this. Though infrequently collected, both species appear to be widely distributed within the 15–25 cm isohyets south of 25° S latitude.

Discussion

There are no consistent venational, genitalic or other structural differences which justify the separation of *Thalainodes* Lower and *Macqueenia* Turner from *Thalaina* Walker.

The presence of an areole in the forewing is not correlated with any other features of diagnostic value beyond species level. An areole is present in one form in *selenaea*, in another form in *chionoptila*, *clara* and *inscripta* and is absent in the rest. Lower's impression of a longer cell in the hindwing of his *Thalainodes* is erroneous as measurement will show.

Some diversity exists in the male antennae: they are laminate with ventrally produced, ciliated segments in *selenaea*, *inscripta* and *clara*, shortly bipectinate in *angulosa*, *macfuitlandi* and *kimba*, and strongly bipectinate in *allochroa*, *paronychia*, *chionoptila* and *tetraclada*. Earlier authors have previously overlooked the slight but definite bipectinate nature of the antennae of *angulosa*.

The corneous frontal process appears to have arisen independently several times in the genus, as it has in many other arid zone genera. This structure, in conjunction with the foretibial spines in *allochroa*, *paronychia* and *kimba*, probably assists the imago to find its way to the surface of the soil after emerging from the buried pupa.

A number of biological features are shared. All are late summer to late autumn

flies with an annual life-cycle. It is very likely that eggs of all species are stimulated to hatch by rain as *angulosa* is (McFarland 1973). Larvae are associated with *Acacia* (or less often *Cassia*) and where known, complete their feeding in early spring and pupate just below the surface of the ground where they overwinter. Pupal aestivation is a phenomenon shared by many autumn-flying cinnomines in southern Australia, such as the species of *Chlenias* (Madden & Bashford 1977). *Thalaina* has successfully exploited a very wide range of habitats in the southern half of Australia, a few species having adapted to each major ecological zone within the overall range of the genus.

Previous attempts to fragment the genus have been based on either incorrect evidence or are unnecessary, since several other genera (e.g. one to contain *allochroa* and *paronychia*) could be erected on similar evidence. Therefore, I feel it is better to slightly expand the original definition of *Thalaina* to contain all of the above species, thus reflecting their close relationship.

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A NEW SPECIES OF MANAYUNKIA (POLYCHAETA) FROM EPHEMERAL LAKES NEAR THE COORONG, SOUTH AUSTRALIA

BY PAT HUTCHINGS, PATRICK DE DECKKER & MICHAEL C. GEDDES

Summary

The polychaete *Manayunkia athalassia* n.sp. is described from ephemeral lakes adjacent to the Coorong Lagoon, South Australia. This is the first record of this genus from Australia. *Manayunkia athalassia* is active over a wide range of salinities (27-95‰) and persists in dry lake beds during the summer months.

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by PAUL HUTCHINGS², PATRICK DE DECKKER¹ & MICHAEL C. GEDDES³

Summary

HUTCHINGS, P., DE DECKKER, P. & GEDDES, M. C. (1981) A new species of *Manayunkia* (Polychaeta) from ephemeral lakes near the Coorong, South Australia. *Trans. R. Soc. S. Aust.* 105(1), 25-28, 12 June, 1981.

The polychaete *Manayunkia athalassia* n.sp. is described from ephemeral lakes adjacent to the Coorong Lagoon, South Australia. This is the first record of this genus from Australia. *Manayunkia athalassia* is active over a wide range of salinities (27-95‰) and persists in dry lake beds during the summer months.

Introduction

The fauna of athalassic (non marine) saline lakes in south-eastern Australia has been listed in several studies (Bayly & Williams 1966, Bayly 1970, Geddes 1976, Williams 1978, De Deckker & Geddes 1980). The only record of polychaete worms is from a small lake near Lake Eliza, South Australia where *Ceratonereis erythraeensis* Fauvel and *Capitella capitata* (Fabricius) were collected (Bayly 1970). These species are known to tolerate a wide range of salinities but cannot resist desiccation. During a recent study of 23 ephemeral lakes near the Coorong Lagoon, South Australia (De Deckker & Geddes 1980) another polychaete, a new species of *Manayunkia*, was common in several localities.

Manayunkia athalassia n. sp.

FIG. 1

Type material

Holotype (Aust. Mus. W17671) from ephemeral lake at 36°19'46"S, 139°44'48"E, adjacent to Coorong, S.A., coll. P. De Deckker & M. C. Geddes 17.vii.1978.

Paratypes from various ephemeral lakes adjacent to Coorong (20 specimens, AM W17672), United States National Museum (1 specimen USNM 63370), British Museum (Natural History) (1 specimen ZB 1980: 265). Further material in Australian Museum (9 specimens AM W17677).

Tentacular crown colourless, anterior body up to setiger 3-5 darkly pigmented, rest of body colourless. Thorax of eight setigers,

abdomen of three setigers. All thoracic setigers similar in size, abdominal setigers equal in length, slightly shorter than thoracic setigers. Tentacular crown of paired symmetrical halves with semicircular bases, each half with two short compact radioles. Outer radiole with four short stumpy pinnules and inner radiole with three, originating close to the base of the radioles. Radioles ciliated and not connected by web-like membrane. Ventral paired palps vascularised, smooth and with skeleton; palps, thicker than radioles but similar in length. Prostomium bluntly rounded with pair of pigment eye spots, visible only after removal of tentacular crown. Peristomial collar well developed ventrally, triangular with rounded apex; collar developed laterally as narrow rim and present dorsally as two small lappets. Setiger 1 with notosetae only, subsequent setigers with noto- and neurosetae. Notosetae of two kinds, basically broad bladed capillaries and hastate setae: thoracic neurosetae long handled hooks, abdominal neurosetae long handled uncini with six or seven horizontal rows of teeth, each row with four or five teeth, teeth not perfectly aligned in rows, fewer teeth per row towards apex. Number of noto- and neurosetae per setiger shown in Table 1. Triangular pygidium with no pygidial eye spots.

Length of holotype 5 mm, paratypes 3-4 mm. Width of holotype 0.5 mm, paratypes 0.4-0.5 mm.

Ecology

Manayunkia athalassia occurs in ephemeral, athalassic, saline lakes adjacent to Coorong Lagoon, South Australia. The lakes, in which *M. athalassia* occurs, are not connected to the sea, and are characterised by fluctuating salinities and varying water levels, due to the raising and lowering of the saline water

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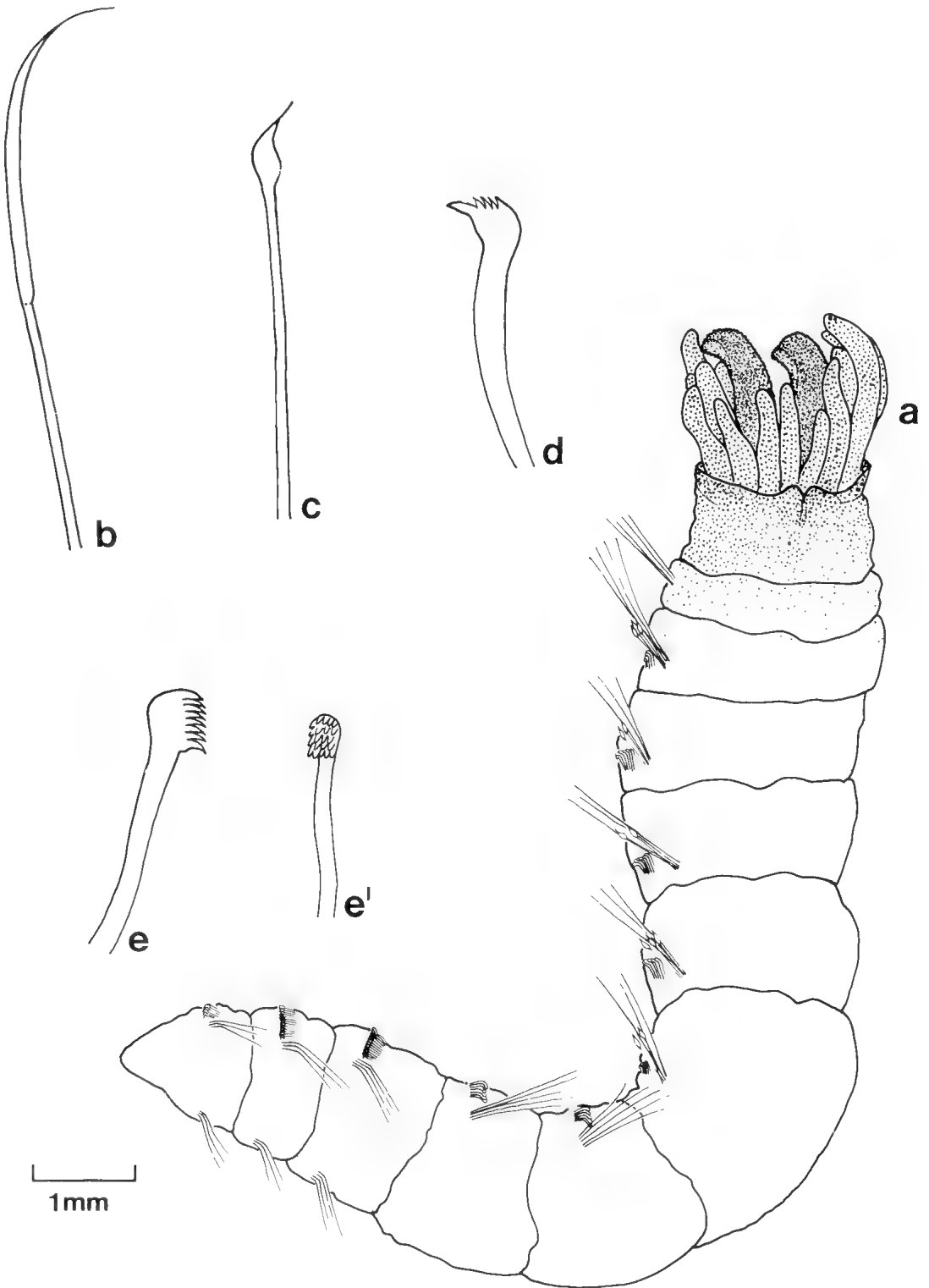


Fig. 1a. *Manayunkia athalassia* n.sp. entire animal, dorsal view, b. capillary seta, c. hastate thoracic seta, d. thoracic neuroseta, e. abdominal neuroseta, lateral and head on view.

TABLE 1. Number of notosetae and neurosetae per setiger.

Setiger	Notoetae		Neurosetae	
	capillaries	hastate	(all uncini)	
Thoracic	1	4	1	absent
	2	3	2	4
	3	3	3	4
	4	3	2	4
	5	3	2	4
	6	3		3
	7	5		2
	8	5		4
Abdominal	1	3		10
	2	3		12
	3	3		11

table and to seasonal precipitation. A description of the physical and biological features is given by De Deckker & Geddes (1980). The polychaetes collected by Bayly (1970) were not found in this study.

Manayunkia athalassia lives in translucent gelatinous tubes, in soft clayey carbonate sediments which some times contain shell debris (ostracods, gastropods). Occasionally *M. athalassia* was found living in a colony of up to 20 individuals. Empty gelatinous tubes also were found.

This species certainly persists in the lake beds while lakes are dry over the summer months. Even when the lakes are dry some moisture may be trapped by hygroscopic salt crystals, and an occasional cover of dead aquatic plants such as *Lepilaena* sp. and *Ruppia* sp. and, less frequently, the alga *Lamprothamnion papulosum* on the surface of the mud. However, the summer air temperatures may exceed 40°C. In February 1979 distilled water was added to samples of mud collected from dry lakes where *M. athalassia* occurred the previous season. Within one day active adults were seen at the wide range of salinities of 27–95‰. Further laboratory studies showed that it could be maintained in an aquarium of 82‰ for several months.

Comments

Manayunkia athalassia differs from congeners in being found in ephemeral saline environments isolated from the sea; the other species are found in marine or brackish water conditions. *M. brasiliensis* Banse, 1956 collected in mangroves in Canaã in Brazil may experience some hyper-marine salinities in the

interstitial water during low tide, but no salinity measurements are given.

Manayunkia athalassia also differs morphologically from the other species. *M. caspica* Annenkova, 1928 has six or seven pinnules per radiole and *M. speciosa* Leidy, 1859 has six radioles with about 60 pinnules per radiole. Southern (1921) suggests that the arrangement of the filaments, which appear to be attached in groups to a short common stem, is an artifact and probably due to the contraction of the basal membrane. However, we suggest that the filaments arise from a short common stem as in congeners, but we have not examined the type. *M. polaris* Zenkewitsch, 1935 has equal numbers of pinnules on both radioles, whereas *M. athalassia* has three pinnules on the inner and four on the outer radiole. *M. aestuarina* (Bourne 1883) has four pinnules per radiole with the paired palps considerably longer than the pinnules, whereas in *M. athalassia* the palps and the pinnules are similar in length.

Detailed setal counts are given only for *M. brasiliensis* and *M. polaris*. *M. brasiliensis* has more setae of all kinds on both abdominal and thoracic setigers than *M. athalassia*. In addition *M. brasiliensis* has capillary setae of two different lengths whereas *M. athalassia* has all capillary setae of similar length. *M. polaris* has considerably more abdominal uncini than *M. athalassia*. For these reasons *M. athalassia* is described as a new species. The specific name refers to the type of saline lakes in which this species lives.

Only three genera of the subfamily Fabriciinae have been recorded from Australia: *Desdenoma*, *Fabricia* and *Oriopsis* (Day & Hutchings 1979). Hartmann-Schroeder & Hartmann (1979) have described an *Oriopsis* sp. and Fabriciinae gen. and sp. indet. from Port Hedland, Western Australia. *Manayunkia athalassia* is the first record of this genus from Australia, but several other species of the subfamily Fabriciinae are present in Australia and shortly will be described by Hutchings. Earlier, general marine collections overlooked the Fabriciinae because they are small and often have specialised habitat requirements.

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DISTRIBUTION OF PINNA BICOLOR GMELIN (MOLLUSCA: BIVALVIA) IN SOUTH AUSTRALIA, WITH OBSERVATIONS ON RECRUITMENT

BY A. J. BUTLER & M. J. KEOUGH

Summary

A diving survey was conducted in January 1980 at 43 sites from Port Broughton in Spencer Gulf to Ceduna in the Great Australian Bight, to observe the distribution of the bivalve *Pinna bicolor* Gmelin, its density, habitat-types and associated species. Earlier records from Investigator Strait, Gulf St Vincent and Spencer Gulf are also reported. At 11 sites samples were taken to determine distributions of shell length, counts of growth checks and gonad states.

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Summary

BUTLER, A. J. & KEOUGH, M. J. (1981) Distribution of *Pinna bicolor* Gmelin (Mollusca: Bivalvia) in South Australia, with observations on recruitment, *Trans. R. Soc. S. Aust.* 105(1), 29-39, 12 June, 1981.

A diving survey was conducted in January 1980 at 43 sites from Port Broughton in Spencer Gulf to Ceduna in the Great Australian Bight, to observe the distribution of the bivalve *Pinna bicolor* Gmelin, its density, habitat-types and associated species. Earlier records from Investigator Strait, Gulf St Vincent and Spencer Gulf are also reported. At 11 sites samples were taken to determine distributions of shell length, counts of growth checks and gonad states.

Although *P. bicolor* is widespread in suitable habitats throughout South Australia, its distribution is 'patchy' on large and small scales. Recruitment is shown to vary in space and time and the significance of this in the ecology of the species is discussed.

Introduction

The ecology of *Pinna bicolor* Gmelin is of intrinsic and practical interest (Butler & Brewster 1979) and we have been studying both the population ecology of the bivalve (Butler & Brewster 1979) and the epibiota on its shells (Kay & Keough 1981, Keough 1981¹) at a few sites in Gulf St Vincent. However, there is no systematically collected information about the distribution and habitat-types of this species throughout the rest of the State.

It is well known that the 'recruitment' of many marine organisms, especially those with pelagic larvae, is variable in both space and time. By 'recruitment' we mean entry to the population at a size such that they can be detected or captured—in this case, seen by a diver. This is not the same as 'settlement' from the plankton, because newly-settled larvae may die before they are detectable. Variability in recruitment may be extremely important in the ecology of such species (e.g. Bowman & Lewis 1977, Keough¹, Sutherland 1974, Sutherland & Karlson 1977). Although variability in recruitment is reasonably well documented for certain commercially important species (e.g. Loosanoff 1966, Andrews 1979) there is a paucity of published data about its occurrence in a wide variety of organisms, and a paucity of detail about the spatial and temporal scales of 'patchiness' in recruitment.

Such data are needed for the development of methods for investigating patchy recruitment, and for the development of models, and management policies, for species which have large random variation in certain components of their environments.

Pinna bicolor is such a species, and in South Australia it is at the southern edge of its tropical and subtropical range (Rosewater 1961), so it is especially interesting to know how its recruitment varies between places and times in South Australia.

Finally, the spatial distributions of sessile, benthic animals may be 'patchy' in the sense that their density appears to be non-uniform and to vary non-randomly over areas that appear to an observer to be uniformly suitable (e.g. various papers in Coull 1977). It is, of course, possible that the area is not in fact uniformly suitable, but also possible that the animals are absent from some habitable sites, perhaps as a result of 'patchy' recruitment. Again, this phenomenon requires documentation as a first step in its study. It is important to produce distribution maps showing confirmed absences as well as records of a species.

This paper reports a survey designed to provide general observations on the distribution of *P. bicolor* in South Australia, the habitat-types in which it occurs, the organisms associated with it and the regularity of its recruitment. Certain conclusions can be drawn from these general observations made at one time; detailed explanations must depend upon long-term observations and experimental tests of hypotheses.

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† Keough, M. J. (1981) Dynamics of the epifauna of the bivalve *Pinna bicolor* Gmelin. Ph.D. thesis, University of Adelaide (submitted).

Methods

Pinna has been recorded from depths as great as 30 m on the floor of Gulf St Vincent (Shepherd & Sprigg 1976) but this survey was confined to areas within 2 km of the shore and depths no more than 18 m. Our object was to visit as many as possible of those sites where *Pinna* had been reported or where it might have been expected to occur from the type of bottom and degree of exposure. Our assumption was simply that *Pinna* requires a soft bottom and no more than moderate wave-exposure. That part of the South Australian coast from the Victorian border to Backstairs Passage is not discussed here. Before this survey we had many records from Gulf St Vincent and some from Spencer Gulf and Investigator Strait; those records are summarised here, and in particular we discuss data from eight sites scored within two months of the main survey and using the same procedures (sites 1-8 in Table 2). The survey itself covered 43 sites from Port Broughton in Spencer Gulf to Ceduna in the Great Australian Bight in January, 1980.

Subtidal sites were surveyed using SCUBA from an inflatable dinghy. Intertidal sites on foot. At every site, position was determined by landmarks and bearings, and a map reference recorded. Depth was measured in m by shot-line, surface and bottom water temperatures in °C by mercury thermometer, and the state of tide and current noted. An estimate was noted of prevailing wave and current conditions, judged from aspect, present conditions and weather, bottom topography and surroundings.

The diver swam over a variable (but always recorded) distance, making notes on a prepared data-slate. He recorded a qualitative statement of bottom type and dominant macrobiota and estimated percentage cover for each of the seagrass genera *Zostera*, *Posidonia*, *Amphibolis* and *Halophylla*. The density of *P. bicolor* was estimated separately for each of two size-classes (dorso-ventral shell height ≤ 7 cm, and height > 7 cm in No. m⁻²). The observer carried an aluminium rod 1 m long to remind him of scale, and had extensive prior experience of measuring density using a 1 m² quadrat, and so the estimates can be taken as sufficiently reliable for use as an index of density. The smaller size-class is likely to have settled within the last year (Butler & Brewster 1979); it was scored separately to give an index of recruitment at sites where samples were not taken. He also

noted qualitatively the size distribution, spatial distribution, morphology and epibiota of *P. bicolor*. Densities of the animal species or groups listed below were scored on the following qualitative scale: none seen, rare, common, abundant. These categories were based on previous experience of 'typical' densities for these species, and have different meanings for each group. The groups scored were: the bivalves *Mallemus meridianus*, *Chlamys asperimus*; and *C. bifrons*, gastropods of the genus *Polinices* and family Muricidae, holothurians, echinoids, asteroids, fish and cephalopods. Under the headings Muricids, Urchins and Asteroids, and commonly under others, it was possible to identify the particular species recorded.

At certain sites, which are marked with asterisks in Table 1, in addition to all the above observations, random samples of *P. bicolor* were collected by clearing a 1 m-wide transect in a randomly-chosen direction, and examined in the dinghy or ashore. For each animal, antero-posterior shell length and dorso-ventral shell height were measured as described by Butler & Brewster (1979). Scars left by the posterior adductor muscle in the nacreous layer of the shell were counted: these are counted with error, but the number of 'major' scars appears to be an index of age (Butler & Brewster 1979) and in this study they were always counted by the same observer. A crude index of age is also available from the epibiota of the shell, given a knowledge of the biology of the epibiotic species (Keough¹), which were recorded in this study on the qualitative scale used by Butler & Brewster (1979) with notes on species-composition. The reproductive tissue in *Pinna* spreads diffusely under the mantle anterior to the posterior adductor muscle and is not always detectable macroscopically. Its development is as yet poorly understood. In this study it was scored qualitatively on the following scale: 0, none visible; P, poorly developed, a thin layer of what appears to be gonad visible; M, moderately developed, undoubtedly gonad tissue present obscuring underlying organs; W, well developed, massive gonad concealing large area of underlying organs.

Finally, for each animal we noted shell damage due to breakage or sponge boring, and the presence of sububular spines on the exterior of the shell. Table 1 shows the sites investigated. In addition to visiting widely spaced locations, we commonly sampled

TABLE 1. Sites inspected and estimated densities of *P. bicolor*, summer, 1979-80. *Random samples of *P. bicolor* were collected for measurements, etc. at these sites. †Densities at these sites were measured using a 1 m² quadrat. Density columns are left blank for sites where no *Pinna* was found. S: *P. bicolor* of $H \leq 7$ cm. L: *P. bicolor* of $H > 7$ cm.

Site No.	Location	Depth (m) (1-intertidal)	Lat °S/ Long. °E	S No. m ⁻²	L No. m ⁻²
1	1-2 km W of Semaphore jetty	7	34.83/138.45	1.8	2.5
2*	3 km NW of St Kilda	3	34.73/138.48	0	<<0.1
3*†	2 km E of Ardrossan	15	34.43/137.95	1.87	0.97
4	Ardrossan: beacon N of bulk loading jetty	7-8	34.43/137.93	0	0.2
5*†	Stansbury: on intertidal sand-spit	1	34.92/137.83	1.71	1.41
6*†	Edithburgh: site of Butler & Brewster (1979)	7	35.11/137.78	0.20	1.54
7	Troubridge Island: intertidally on SW side	1	35.13/137.82	0.30	>1
8	Wallaroo: to 150 m W from site of old jetty	0.7	34.93/137.61	2	5
9	Port Broughton: over 4 km travelled in channel and around mangrove island	0-3	33.56/137.92		
10	Chinaman Creek: 2 km WSW of shacks	10.5	32.23/137.80		
11	Chinaman Creek	4	32.65/137.80		
12	1.5-2 km WSW of Chinaman Creek	4.5	32.65/137.78		
13*	400 m WSW of Chinaman Creek	3-4	32.68/137.83	10	5
14	Chinaman Creek	2-3	32.65/137.82		
15	Port Augusta: Playford Power Station jetty	7-10	32.54/137.78	<0.01	4
16*	Port Augusta: first normal channel marker S from Power Station	7.5	32.55/137.78	0.01	0.8
17	Franklin Harbour: ca. 400 m S of Cowell jetty	3	33.70/136.94		
18	Franklin Harbour	3-4	33.70/136.94		
19	Franklin Harbour: 500-600 m E of jetty	4	33.68/136.95	0	<0.01
20	Franklin Harbour: Cowell jetty	4-5	33.68/136.94		
21*	Franklin Harbour: (locally called Dr Thompson's Reef)	0.5	33.71/136.94	0.01	0.85
22	Tumby Bay: 600 m ESE of jetty	5.5	34.39/136.12		
23*	Tumby Bay: jetty	4	34.39/136.11	0.05	0.15
24	Tumby Bay: 200 m off end of jetty	5	34.39/136.12		
25*	Tumby Bay: 100 m off entrance to caravan park	1	34.38/136.11	2	7
26*	Port Lincoln: 300 m E of caravan park jetty	13.5	34.73/135.89	0	0.7
27	Port Lincoln: Kerton Point jetty	9	34.72/135.88	0.001	0
28	Port Lincoln: 150 m off caravan park	3-5	34.73/135.89		
29	Port Lincoln: 300 m WSW of 1st port channel marker	15-18	34.70/135.88		
30	Port Lincoln	13	34.72/135.87	0	0.001
31	Coffin Bay: between jetty and point to NW	2.5	34.63/135.47		
32	Coffin Bay: in channel leaving Coffin Bay	4	34.62/135.46		
33	Coffin Bay	1	34.62/135.46		
34	Coffin Bay: between Goat Is. and other side of bay	5	34.62/135.47		
35	Coffin Bay: point at entrance to Coffin Bay	2.5	34.62/135.46		
36	Kellidie Bay	1-2	34.61/135.48		
37	Kellidie Bay	1	34.61/135.47		
38	Coffin Bay jetty	4	34.62/135.47		
39	Elliston: near jetty	5	33.64/134.89		
40	Venus Bay: near jetty	3-4	33.23/134.68		
41	Venus Bay	1	33.23/134.72		
42	Venus Bay: downstream from 2nd upstream channel marker	3	33.22/134.68		
43	Venus Bay: side channel on way back to jetty	4	33.23/134.68		
44	Venus Bay: 1st upstream channel marker from jetty	0.5-4	33.22/134.67		
45	Venus Bay: channel SW of Germein Island	0.5-3	33.22/134.66		
46	Venus Bay	5-6	33.23/134.64		
47	Venus Bay: 1st downstream channel marker from jetty	3	33.23/134.66		
48*	Streaky Bay	1	32.80/134.21	14	3.5
49	Streaky Bay: 100 m inshore from 48	1	32.80/134.21	3.5	1
50*	Streaky Bay: 200 m S of 1st outgoing channel marker, near Crawford Landing	6.5	32.78/134.23	1.5	1.5
51	Ceduna jetty	3	32.13/133.67	1	1

several sites separated by short distances within one area or embayment. Since one object of the survey was to investigate the small-scale 'patchiness' of *P. bicolor*, and since one object of this paper is to allow future workers to investigate changes over time, the locations of our sites are given in as much detail as possible in Table 1.

Distribution in South Australia

Pinna bicolor has been recorded by us at the locations for which positive densities are given in Table 1 and from Fishery Beach (Fleurieu Peninsula), American River Inlet near Muston (Kangaroo Island), Rapid Bay, Aldinga Reef and Price (all Gulf St Vincent), Goose and Wardang Islands (Spencer Gulf). Shepherd & Sprigg (1976) recorded it at many sites on the floor of Gulf St Vincent, and Cotton (1961) recorded it from "Beachport to Fremantle". Thus, the species is widespread on sheltered shores or in deeper water throughout the State. However, note that *P. bicolor* was not found at all of the locations in Table 1 and that sites close to one another often differ (e.g. Chinaman Creek, sites 10-14; Franklin Harbour, sites 17-21; Tumby Bay, sites 22-25; Port Lincoln, sites 26-30). Note also that in some embayments which appeared suitable for *Pinna*, we found none (Kellidie Bay, sites 31-38; Venus bay, sites 40-47; Elliston, site 39) or very few (Franklin Harbour, sites 17-21; Port Lincoln, sites 26-30). Thus, the distribution of *P. bicolor* appears 'patchy'.

Morphology

A few shells found at various sites were similar to the species which Cotton (1961) identified as *Subtopinna virgata*, but almost all were typical of his *Pinna dolabrata*. Both of these were referred by Rosewater (1961) to the variable species *P. bicolor*. The relationship between shell length and shell height will be discussed elsewhere, but on preliminary analysis it appears not to differ significantly amongst all the locations sampled. At any location some shells bore more subtrihedral spines than others; these were more prominent in young individuals; the typical form at all locations is fairly smooth-shelled (Cotton 1961, Figs 68 & 69; Rosewater 1961, Pl. 147, 151 & 152).

Density in different habitats

This survey did not provide data suited for powerful tests of null hypotheses about the relationship between *P. bicolor* density and such

variables as bottom type, depth, current and the presence of other organisms. Nevertheless, some extreme possibilities can be eliminated from the available data. Table 1 shows estimated densities at those sites where *P. bicolor* was found. *P. bicolor* occurred in bottom sediments ranging from very fine sand to very coarse sand; we could detect no relationship between our qualitative notes on sediment type and the presence, or density, of *P. bicolor*. The 'prevailing' or 'average' conditions of temperature and current could only be estimated roughly from our measurements and notes on a single dive, but again we could not see a possible explanation for the presence, density, or estimated age-distribution (see below) of *P. bicolor* in either of these variables.

There is no significant correlation between *P. bicolor* density and depth (data in Table 1 for positive *P. bicolor* densities; zero densities included for all other sites; $r = -0.17$, $n = 51$, $P > 0.05$), nor between *P. bicolor* density and the percentage cover of seagrasses (the latter transformed to angles, Rohlf & Sokal 1969, p. 129; $r = 0.02$, $n = 51$, $P > 0.05$). Since we already had reason to suspect a negative correlation between *P. bicolor* and seagrasses (unpublished data), this was rechecked by excluding data pertaining to embayments where *P. bicolor* was rare or absent, and where one might argue larvae have, for some reason, failed to arrive (namely Pt Lincoln, Kellidie Bay, Venus Bay and Elliston). The correlation between *P. bicolor* density and seagrass cover remained non-significant ($r = -0.17$, $n = 29$, $P > 0.05$).

There was no significant correlation between *P. bicolor* density and latitude. (For sites with positive densities, $r = 0.37$, $n = 22$, $P > 0.05$; for all sites, $r = 0.17$, $n = 51$, $P > 0.05$.)

The densities of other species which might conceivably influence *P. bicolor*, or have similar requirements, were scored on qualitative scales. The reasons for scoring these species were as follows. The bivalves *M. meridionalis*, *C. asperianus* and *C. bilirons* are ecologically similar to *Pinna*. Certain asteroids prey on *P. bicolor*. The gastropods *Polinices* spp. and probably some muricids are thought to do so. Some fish and cephalopods may do so, especially on small *Pinna*. Holothurians and echinoids may influence the survival of recently-settled post-larvae. We were interested in any hint of associations (positive or negative) between the presence of *P. bicolor*, particularly of recent recruits, and the

TABLE 2. Association between qualitative scores for the densities of *P. bicolor* and three species of epibenthic bivalves. Each figure in the Table is the number of sites at which that combination of scores occurred.

Density of <i>P. bicolor</i>	<i>Mallemus meridianus</i>		<i>Chlamys asperrimus</i>		<i>Chlamys bifrons</i>	
	low	high	low	high	low	high
low $\leq 1 m^{-2}$	34	5	39	0	37	2
high $> 1 m^{-2}$	5	3	7	1	6	2
χ^2 for 2×2						
1 contingency table	1.38		0.79		1.30	
P	>0.05		>0.05		>0.05	

abundance of any of these species. Inspection of a table of these scores showed no obvious relationships with *P. bicolor* density. Most of the data do not warrant statistical analysis, but the association between the bivalves *P. bicolor*, *M. meridianus*, *C. asperrimus* and *C. bifrons* was examined further. Scores for each species were grouped into two categories—'low' (= 0 + rare) and 'high' = (common + abundant)—and the scores for *P. bicolor* were tested for independence of each of the other species in three 2×2 contingency tables; none was significant at the 5% level (Table 2). This is not a powerful test; it merely indicates that the other species are not strongly associated with *P. bicolor*.

Gonad condition at different sites

The scoring of gonad development as None, Poorly, Moderately or Well Developed is a very crude index, not only because it is somewhat subjective, but also because the histology of gonad development in *P. bicolor* has not yet been established and related to these scores. (This work is in progress.) Nevertheless, if the populations at different sites were predominantly in different stages of the reproductive cycle, this might be expected to be reflected in the scores, whatever their detailed histological meanings. To test this, we first determined for each of the 12 sites at which gonads were examined within the time-period December 1979-January 1980, the minimum number of adductor muscle scars at which any animal was scored 'moderately' or 'well developed' (M or W). Next, we considered only animals with that number of scars or more, and calculated the proportion of them scored M or W. This was done because at some sites the proportion of the whole sample with developed gonads would be depressed by the presence of a large number of very small, pre-reproductive animals. Scar counts are used here as an index of age (see below) but similar results are obtained if shell length, in-

stead of scars, is used to determine which animals are potential breeders.

The results are shown in Table 3. The proportions scored M and W show highly significant heterogeneity between sites when the whole set is tested as a 2×12 contingency table. However, this may possibly be due to the length of time (more than one month) between sampling the first and last sites. Therefore, consider only the seven sites sampled over 10 days (5-15.1.80) and sampled sequentially from Franklin Harbour to Ceduna so that latitude rose and then fell during the period. This set is also highly significantly heterogeneous.

There are three pairs of sites sampled close together in both time and space; sites 13 & 16 in Upper Spencer Gulf, sites 23 & 25 in Tumby Bay and sites 48 & 50 in Streaky Bay. Tested by a 2×2 contingency table, each of these pairs is homogeneous for the proportion M or W. The proportions scored M and W (transformed to angles) are not significantly correlated with latitude ($r = 0.03$, $n = 12$, $P > 0.05$). In summary, despite our crude method of scoring gonad condition, it is clear that sites spatially far apart, even if sampled at about the same time, differ in the proportion of animals in breeding condition. Sites close together in space and time receive similar scores.

Counts of adductor muscle scars

Adductor muscle scars are counted with error, but Butler & Brewster (1979) argued, for site 6, Table 1, that major scars probably represent winter growth checks. This awaits confirmation from current work on tagged animals, and it is also important to note that variables which cause a slowing of growth, such as temperature, food supply, breeding or various kinds of stress (Clark 1974), may be distributed differently at different sites. At one site, scar counts are probably an index of age,

TABLE 3. Gonad development in *Pinna bicolor* sampled at 12 sites. Site numbers correspond to Table 1. Gonads were visually scored as 'O'—not apparent; 'P'—poorly developed; 'M'—moderately developed and 'W'—well developed; these have been pooled into two categories here. Only animals in reproductive "age"-class, as determined by adductor muscle scars, are included (see text).

Site	Date Sampled	Number O + P	Number M + W
3	18.xii.79	0	49
5	20.xii.79	27	131
6	13.xii.79	20	130
13	24.i.80	16	39
16	23.i.80	19	57
21	5.i.80	0	74
23	7.i.80	11	19
25	6.i.80	23	42
26	9.i.80	24	25
48	13.i.80	11	43
50	13.i.80	6	22
51	15.i.80	5	43

χ^2 tests for homogeneity:

Whole 2 × 12 table: $\chi^2 = 84.92$ ($P < 0.001$)

Sites 21,23,25,26,48,50,51: $\chi^2 = 54.13$ ($P < 0.001$)

Sites 13,16: $\chi^2 = 0.10$ ($P > 0.05$)

Sites 23,25: $\chi^2 = 0.01$ ($P > 0.05$)

Sites 48,50: $\chi^2 = 0.01$ ($P > 0.05$)

but they do not necessarily estimate chronological age in the same way at all sites. We know that the relationship between shell length and scar count differs between sites. For example, the average length of animals with five scars from site 3 is 31.5 cm; that from site 5 (which is intertidal) is 20.0 cm. We have at present no way to test whether intertidal animals produce more scars per unit time, or simply grow more slowly. However, from the data available to Butler & Brewster (1979) and various observations obtained subsequently (Butler unpublished) it seems likely that scars do provide an estimate of age in years, in several different habitats (sites 3, 5, 6, 7 in Table 1). We shall therefore base our interpretation of scar counts on this assumption.

If the number of major adductor scars is an estimate of age in years, then even though scars are counted with error a comparison of the distributions of scars counts from two sites should test whether the age distribution is the same at the two sites. The distributions of scar counts at 13 sites are shown in Table 4. They are highly significantly heterogeneous when the whole set is tested, or when only the set sampled in January 1980 is tested (see G-values in Table 4). Comparing pairs of sites close together in space and sampling date, we find

TABLE 4. Frequencies of counts of adductor-muscle scars in samples of *P. bicolor*.

Site	0	1	2	3	4	5	6	7	8	9	10	11	≥12	No. of animals in sample
2		3	24	17	3	3	1	1	2		2			56
3	105		3	4	1	1	1	3	1	2	3	3	27	154
5	6	6	22	29	21	16	14	21	9	10	4	3	3	164
6		33	28	15	21	9	17	7	8	11	1			150
13		7		3	2	12	10	13	7		6	2		62
16		3	4	11	21	16	10	7	3	5	2		1	83
21		1	3	4	15	20	14	12	3	1	1	1		75
23			1	10	2	5	3	1	3	2	1	1	2	31
25	2	2	14	7	15	22	9	9	2	1	1			84
26									1	1	4	13	30	49
48	12	9	8	8	6	8	12	8	2	2				75
50	9	13	1	3	4	3	3	6	1	2	4		1	50
51	9	13	7	7	12	3	4	3	3	3	2	3	1	70

Log-likelihood ratio tests for heterogeneity:

Whole 13 × 13 table: $G = 115.6$

Sites 13–51: $G = 499.9$

Sites 13 & 16: $G = 24.15$

Sites 23 & 25: $G = 28.57$

Sites 48 & 50: $G = 14.87$

Scar classes 0–5 (0 & 1 pooled)

All sites except 26: $G = 463.8$

Sites 13–51 (except 26): $G = 153.5$

Sites 13 & 16: $G = 18.42$

Sites 23 & 25: $G = 16.73$

Sites 48 & 50: $G = 7.45$

d.f. = 144

d.f. = 96

d.f. = 7

d.f. = 6

d.f. = 8

d.f. = 44

d.f. = 28

d.f. = 4

d.f. = 4

d.f. = 4

$P < 0.001$

$P < 0.001$

$P < 0.005$

$P < 0.001$

$P > 0.05$

$P < 0.001$

$P < 0.001$

$0.001 < P < 0.005$

$0.001 < P < 0.005$

$P > 0.05$

TABLE 5. Inferences about density of recent recruitment and regularity of recruitment over previous 5-6 years, based on counts of adductor muscle scars (Table 4) on assumptions that scars represent winter growth checks, and that post-recruitment mortality rates and their year-to-year variations are same at all sites. See text for methods. O, no recruitment; m, minor recruitment; M, major recruitment; I, irregular; R, regular. Table also shows inferences about density of recent recruitment based only on diver's estimate of density of *Pinna* of $H \leq 7$ cm at sites where *Pinna* density was > 0 , (Table 1). 0, density = 0; S, sparse, $0 < \text{density} \leq 0.1 \text{ m}^{-2}$; D, dense, density $> 0.1 \text{ m}^{-2}$.

Site	1978-9 recruitment from scar counts	Regularity of recruitment from scar counts	Recent recruitment from density of small animals
1			D
2	m	I	O
3	M	I	D
4			O
5	m	R	D
6	M	I	D
7			D
8			D
13	m	I	D
15			S
16	m	I	S
19			O
21	m	I	S
23	O	I	S
25	m	R	O
26	O	I	O
27			S
30			O
48	M	R	D
49			D
50	M	R	D
51	M	R	D

that one is homogeneous (sites 48 & 50), the other two heterogeneous (sites 23 & 25, sites 13 & 16).

The scar distributions were examined further to make inferences about recruitment. First, we considered the density of recent recruitment. Because of the difficulty in scoring the first, faint scar the categories 0 and one scar were pooled, and assumed to represent 1978-9 recruits. The size of this class relative to the rest of the sample was scored for each site into one of three categories: 0, no animals with zero or one scar; minor, $0 < p < 20$ where p = percentage of the sample having zero or one scar; major, $20 \leq p < 100$. The results are shown in Table 5. As for most animals with planktonic larvae, the density of recruitment is not expected to be constant from year to year, even if some recruitment always

occurs; this appears to be borne out by Table 4. Further, the fluctuations in density of recruitment do not seem to be in phase at all sites. If fluctuations in recruitment were in phase, and if subsequent age-specific mortality rates were also the same, the conspicuous modes should be in the same scar-classes at all sites. They are not, as is shown by Table 4. To test this, we considered only the first six scar-classes (0-5), because for older animals we have less confidence in the assumption of a constant schedule of age-specific mortalities. The results of tests for homogeneity are shown in Table 4. The whole set is highly significantly heterogeneous, as is the set of nine sites sampled in January 1980. More importantly, two of the pairs of nearby sites sampled close together in time are highly significantly heterogeneous (sites 13 & 16 and sites 23 & 25).

Next, we asked whether recruitment appears to be 'regular' at each site, that is, whether some recruits appear each year, albeit at varying densities. To do this, high scar-classes were ignored because mortality may have reduced their numbers so much that sampling error becomes important. The first six scar-classes (0-5) were examined; recruitment at a site was called 'irregular' if there were any zero frequencies in the first six classes, otherwise it was 'regular'. Table 5 shows the result. It also shows a ranking of the diver's estimate of density of small *Pinna*. Note that this is an 'absolute' index based on the number of small animals per m^2 of bottom, whereas the above method is based on the proportion of the sample which was young. Also, an animal 7 cm in shell height may, at some sites, be several years old. The index based on density of small animals is thus of limited value, but is included because it is available where samples were not collected.

The magnitude of the 1978-9 recruitment, on either index, appears to have differed between sites. Many have irregular recruitment. In one case a pair of sites which differed in scar-frequency distributions above (sites 23 & 25) also differ in their 1978-9 recruitment and in their regularity of recruitment.

The data collected concurrently with the samples give no suggestion of explanations for these variations. Neither depth nor percentage cover of seagrass was significantly associated with regularity of recruitment using either the Fisher exact test (assigning seagrass or depth values to two categories) or a two-sample runs

test (ordering the depth or seagrass values and then counting runs of regularity scores); in both cases, $P > 0.05$. Similarly if the scores for 1978-9 recruitment were grouped into two categories (0+m, M) then they were not significantly associated at the 5% level with either depth or seagrass cover using either test.

Regularity of recruitment was not significantly associated with latitude. This was tested by grouping those sites scored I and those scored R and comparing their mean latitudes ($t_{11} = 1.07$, $P > 0.2$).

The magnitude of 1978-9 recruitment (grouped into two categories) was not significantly associated with regularity of recruitment (Fisher exact probability test: $P = 0.085$).

When the notes on associated species were grouped into two categories (0 + rare; common + abundant) and tabulated against the scores for 1978-9 recruitment or for regularity, no positive or negative associations were apparent on inspection, and certainly none was statistically significant at the 5% level using Fisher exact tests.

The density of small animals ($H \leq 7$ cm) is positively correlated with that of larger ones (both estimated *in situ* by the diver). For sites where any *P. bicolor* were found, Pearson's $r = 0.49$, $P < 0.05$; Spearman's $\rho = 0.76$, $P < 0.001$. This test was repeated, excluding sites 5, 7, 13, 21, 23, 25, 48, 49 because their length-scars relationship showed that animal of $H = 7$ cm may have more than two scars, and thus the density of small animals may not be an estimate of the density of recent recruitment. The conclusion remained the same (Pearson's $r = 0.54$, $P < 0.05$; Spearman's $\rho = 0.75$, $P < 0.005$).

However, regularity of recruitment was not significantly associated with total density either by a 2×2 contingency table with density classified as $\leq 2m^{-2}$ or $> 2m^{-2}$ (Fisher exact test: $P = 0.085$) or by a runs test as used above for depths ($P > 0.05$).

Discussion

This survey has provided a distribution map for *P. bicolor* in South Australia. It is based on visits to many sites apparently suitable in having low wave-action with soft bottoms. There is a temptation to assume that when a species has been recorded at two points, it may be expected to occur in suitable habitats in between (thus, distribution maps are often

hatched), but that seems not to be so in this case. The distribution is patchy; *P. bicolor* is absent from some apparently suitable sites. The patchiness occurs on a local scale; *P. bicolor* may be found on some but not other dives on apparently similar bottoms within 1 km or so—e.g., sites 10-14, 17-21, 22-25, 26-30. But it is also evident on a larger scale; the species seems to be absent from certain large and apparently habitable embayments (Kellidie Bay, Venus Bay, Elliston), though present in others north and south of them. Note that these are well-enclosed embayments; perhaps the current patterns are such that the arrival of planktonic larvae there from outside is a rare event. If so, then by chance a recruitment might occur from time to time and establish a temporary 'population'. This seems to have happened at Port Lincoln (site 26). The reason for giving the details in Table 1 is to document this patchiness; later workers might want to check the same locations.

Organisms are rarely if ever distributed evenly. Some of the unevenness in their distributions can be explained by an understanding of their ecology (we can say why the unoccupied sites are unsuitable or have not been colonised), but there may remain a component which cannot be explained, even tentatively, with existing knowledge. The possibility remains that the vacant sites are unsuitable or inaccessible, but the reasons are not at present known. We shall call this 'unexplained patchiness'; *P. bicolor* provides an example.

There is no detectable relationship between density of *P. bicolor* and sediment type, current regime, water depth (Table 1), cover of seagrass, or associated animal species, especially other ecologically similar bivalves (Table 2). One might not have expected a competitive interaction of any importance between these bivalves (Stanley 1977), but perhaps their ecological similarity, or even the fact that *Malleus* and *C. asperimus* use *P. bicolor* for attachment, might have led to a positive association. None is evident. We note in passing that the other three species of bivalves were, like *P. bicolor*, more often scored low than high in density even though many sites appeared suitable, and any diver knows that they can be abundant. These species, too, appear 'patchy'.

Species which are either predators or 'malenitiques' (Andrewartha 1970) might be

expected a *phori* to have most of their influence on younger stages of *P. bicolor*: still, we note that they showed no association with the density of *P. bicolor* large enough to be seen by a diver.

The above is based on imprecise data (mostly subjective rankings) and so there is a possibility that real associations exist but were not detected. However, one might have expected such associations to be at least noticeable in the kind of data we collected, even if they were not statistically significant: no trends, however slight, were apparent. Thus we conclude that with respect to the presence and density of *P. bicolor* we are observing unexplained patchiness.

The proportion of the population with developed gonads appears less 'patchy'. It differs between sites even considering only those sampled close together in time, but spatially-close sites (pairs of sites in the same embayment) do not differ significantly (Table 3). We cannot infer that these populations are in the same phase (because we do not know, for example, whether a gonad scored 'P' is developing or spent) but it seems likely.

Counts of adductor-muscle scars were heterogeneous between sites, including some nearby pairs. These scars probably represent checks in the growth of the animal, but the reasons for the checks, and their periods, are not known with certainty. There is reason to assume that they represent winter growth checks and our interpretation of the counts was based on that assumption. On that assumption, the age-distributions of the standing populations of *P. bicolor* at different sites (including some nearby pairs) differ. We examined these distributions in more detail and found that the proportion of the population with low scar counts (recent recruits) differs between sites including nearby ones (Table 4). In other words, the density of recruits relative to that of adults varies. Further, the presence or absence of whole classes (interpreted as 'regularity' of recruitment) differs between sites. The absence of an entire class is a stringent criterion of 'irregularity', given the error in counting rings. It seems clear that recruitment fluctuates from year to year, and the fluctuations are not in phase at all sites, nor necessarily even at nearby sites. This contrasts with the proportions with developed gonads, which were similar at nearby sites.

Recent recruitment and the regularity of recruitment were not correlated with depth, cover of seagrass, nor with each other. 'Regularity' was not significantly associated with total density of *P. bicolor* as estimated in No. m⁻².

No relationships could be detected between recruitment and the densities of associated species. This is not to say that the associates have no effects. Firstly, it is possible that their abundance is correlated with the recruitment of *P. bicolor* but our data are too imprecise to detect it. Secondly, they may move about, so that their abundance at a particular place and time bears little relationship to their effects on *P. bicolor* there at some earlier time. Thirdly, their effects may be masked by other variables, especially the density of settlement of *P. bicolor*. The lack of correlations in our data does eliminate the grossest hypotheses, e.g. that dense holothurians will, by killing newly-settled larvae, lead to sporadic recruitment.

The above discussion concerns recruits as a proportion of the population. Actual densities of recruits would be of interest. The only relevant data we have are the diver's *in situ* estimates of the densities of two size-classes. The density of small animals is positively correlated with that of large ones, considering all sites where *P. bicolor* were found. However, this may be an artefact, because although an animal of $H \leq 7$ cm at site 3 would very likely be under two years old and probably under one (Butler & Brewster 1979), this will not necessarily be true at all sites (above). However, if we eliminate sites where animals have a large scar count for a given length, we still find the same conclusion: density of small *P. bicolor* is positively correlated with that of large ones. This seems to be rather in contrast to the conclusions drawn above from the scar counts. However, it is consistent with them if the events leading to recruitment are viewed as follows.

Larvae of Pinnidae can travel long distances in the plankton (R. S. and A. Scheltema, *pers. comm.*). Thus, the fact that animals breed at all sites does not guarantee that settlement (still less, recruitment) will occur at all sites, and those larvae which settle at a site may not have been spawned there. Larvae move about with the currents and may well be distributed patchily within the water (see reviews in Steele 1978). Thus, their probability of successful recruitment at a given benthic site

depends firstly on their being carried there on a current of suitable strength, etc. for settlement, and secondly on subtle properties of the bottom (which may vary from time to time), the presence or absence of mobile or ephemeral predators, the availability of food for newly settled post-larvae (which itself may depend upon planktonic patchiness and on the vagaries of the currents), and so on. We stress the term 'probability'. The mere fact that recruitment is partly dependent on currents, on the shapes of land-masses and channels and on the topography of the bottom, will mean that sites differ consistently in the probability that larvae will settle. This can account for some very well-enclosed embayments apparently containing few or no *P. bicolor*, and for a correlation between the densities of adults and young, but it leaves recruitment as a random variable with a large variance which, on the present state of our knowledge, we cannot explain. Most sites receive variable, and some even irregular, recruitment and we cannot explain or predict this using depth, associated species, sediment type or latitude.

Recruitment is a major "mystery stage" (Spight 1975) in the ecology of many species with pelagic larvae (e.g. Andrews 1979, Mileikovsky 1971, Sastry 1979, Underwood 1979). It is important because it varies so widely.

We can hope to understand the ecology of the species after successful recruitment, but recruitment itself is the main event that determines the density of such a species at a given site. Whilst it may be possible in some cases to predict recruitment from independent variables which influence larval survival, our data (especially the very small-scale 'patchiness') give no encouragement that it will be possible in this case. For purposes of a general understanding of the ecology of the system (or for long-term planning, if the species were a commercially important one) we may make use of a probability distribution for recruitment. For purposes of short-term prediction, the only course is to monitor recruitment directly, as done for commercial species (e.g. Brand *et al.* 1980, Phillips 1972, Phillips & Hall 1978).

The above should not be taken as an assertion that nothing can be known about the recruitment of *Pinna*. Knowledge of a probability distribution can be powerful. Those species which interact with *Pinna*—feed on its young, live on its shells, etc.—must be adapted to that probability distribution. It is a challenge to ecology to produce useful models for systems in which many of the important events have probability distributions with large variances.

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THE GIANT RAT-KANGAROO PROPLEOPUS OSCILLANS (DE VIS), (POTOROIDAE: MARSUPILIA) IN SOUTH AUSTRALIA

BY *N. S. PLEDGE*

Summary

Isolated teeth referable to one juvenile *Propleopus oscillans* have been found scattered in a cave deposit at Naracoorte. They have been interpreted as a lower premolar (rP_3); four upper molars : rM^1 (described for the first time), rM^2 , two of rM^3 or 4 ; a lower incisor (lI_1) and four lower molars : lM_2 , rM_3 or 4 , lM_5 , rM_5 . The 'deciduous' molar M^1 is rectangular and quadritubercular, showing greater similarity to the M^1 of *Bettongia* spp. than to *Hypsiprymnodon*. The form of the incisor indicates that this tooth had a period of continued 'rootless' growth until maturity. A large humerus is referred tentatively to *P. oscillans* and body proportions are calculated. *P. oscillans* was an animal of about the same bulk as an Eastern Grey Kangaroo (*Macropus giganteus*), but much stockier and with longer legs. Apparently it inhabited dense scrub, living on a diet of herbaceous vegetation, occasional carrion and small animals.

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PLEDGE, N. S. (1981) The Giant Rat-Kangaroo *Propleopus oscillans* (De Vis), (Potoroidae: Marsupialia) in South Australia. *Trans. R. Soc. S. Aust.* **105**(1), 41-47, 12 June, 1981.

Isolated teeth referable to one juvenile *Propleopus oscillans* have been found scattered in a cave deposit at Naracoorte. They have been interpreted as a lower premolar (iP_3); four upper molars: rM^1 (described for the first time), rM^2 , two of rM^3 or rM^4 ; a lower incisor (Il_1) and four lower molars: lM_2 , rM_3 or lM_3 , rM_4 , rM_5 . The "deciduous" molar M^1 is rectangular and quadritubercular, showing greater similarity to the M^1 of *Bettongia* spp. than to *Hypsiprymnodon*. The form of the incisor indicates that this tooth had a period of continued 'rootless' growth until maturity. A large humerus is referred tentatively to *P. oscillans* and body proportions are calculated. *P. oscillans* was an animal of about the same bulk as an Eastern Grey Kangaroo (*Macropus giganteus*), but much stockier and with longer legs. Apparently it inhabited dense scrub, living on a diet of herbaceous vegetation, occasional carrion and small animals.

Introduction

The kangaroos, wallabies and their allies (the Macropodoidea), contains many species, living and fossil; some are quite common and others exceedingly rare. Modern taxonomists (e.g. Archer & Bartholomai 1978) split this large group into two families: the kangaroos and wallabies in the family Macropodidae, and the rat kangaroos (potoroos, bettongs, etc.) in the family Potoroidae. The latter family is divided into the subfamily Potoroinae, containing potoroos and bettongs, and the subfamily Hypsiprymnodontinae, containing the living Musky Rat-kangaroo *Hypsiprymnodon moschatus* Ramsay and the extinct *Propleopus* species.

Modern *H. moschatus* is a small, rat-like animal living in restricted areas of rain forest in northern Queensland. It is distinguished from other kangaroos by a combination of several primitive characters (Ride 1961, 1964), such as a simple alimentary canal, the presence of the hallux on the inner side of the foot, the presence of an upper canine and a second lower incisor, and relatively simple bunodont molars. These features are combined with a number of specializations. The most striking of these are the large 'plagiaulacoid' premolars, i.e. secant (bladed) premolars, which are larger than the adjacent molars, with a curved and serrated cutting edge, and faces strengthened with a number of parallel, vertical ridges corresponding to the points of

the serrations. Such premolars are, in fact, most distinctive teeth (Woods 1960).

The fossil species of *Propleopus* are believed to be the closest known relatives of *Hypsiprymnodon*. All have large secant premolars, although in *Propleopus* these are more than three times the size of the modern teeth. The molars are also similar. The Mountain Pigmy Possum, *Burrhamys parvus* has similar premolars but a different molar structure and a jaw structure that precludes macropodoid affinities (Ride 1956, 1964). Despite the relatively large size and robustness of the fossil teeth and jaws, however, *P. oscillans* is known from only a handful of specimens. By comparison, kangaroos of similar size from the same deposits often are represented by hundreds of specimens. Nevertheless, occurrences of *Propleopus* are widespread. Woods (1960) listed two specimens, a fragmentary incisor and a near-complete lower jaw, and Bartholomai (1972) described a partial maxilla, from the Eastern Darling Downs.

A further specimen has been reported from Wellington Caves, N.S.W. (Woods 1960) and another from L. Menindee (Tedford 1955, 1967). A second Pleistocene species *P. chillagoensis* has been found in cave deposits at Chillagoe, north Queensland (Archer *et al.* 1978). Archer & Bartholomai (1978) mention a specimen from a Pliocene deposit in northern N.S.W. This dentary may be conspecific with a single isolated molar (Gill 1953, 1957; Ride 1964) from a sub-basaltic Pliocene deposit near Hamilton, Vic., dated at 4.3 million years.

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.

Williams (1980) lists two additional specimens of *P. oscillans*, found recently in South Australia at Hookina Creek (P22425) and near MI Gambier (Green Waterhole, P20815). These have been inspected, but are under study elsewhere so only the cheek-tooth measurements will be given in this paper.

Tooth nomenclature follows the system of Archer (1978): the total dental formula for *Propleopus* would probably be $dI_2^2, I_2^2, dC^1, C^1, P_{2-3}^{2-3}, M_{1-3}^{1-3}$. The first molar M_1 and premolar P_2 are replaced by the erupting P_3 .

New South Australian occurrence

Rich Pleistocene bone deposits are currently being excavated in caves at Naracoorte. These deposits have produced large and varied fossil faunas of mammals, together with associated amphibians, reptiles and birds (Williams 1980). One of these deposits partially filled and sealed a small cave, the Henschke Fossil Cave, that was discovered by quarry operations on the edge of Naracoorte township in 1969. Excavations of the deposit were undertaken by me and continue to yield an abundance of fossil bones. Associated charcoal has been collected, and preliminary radiocarbon results give the deposit an age of around 35 000 years for the upper metre or so of sediment, (SUA-140, depth 105-120 cm, > 35 000 years BP, δC^{13} -997.7 ± 4.0 ; SUA 243, 30-75 cm, 33 800 ± 2400 years BP, δC^{13} -985.1 ± 3.9).

Macropodoids constitute more than half of the Henschke Fossil Cave assemblage, and potoroids are well represented. Amongst

these specimens are several isolated teeth, found over a period of eight years, that may be referred confidently to *P. oscillans*. This small sample comprises one lower premolar (rP_3) and seven molars, one of which I consider to be a deciduous molar (m^1). An unusual lower incisor, by elimination from all other taxa in the assemblage, also appears to be *P. oscillans*. Most of the specimens consist of enamel crowns only. They show little or no wear, indicating a juvenile age for the individual(s) represented. There is no evidence in the form of duplication to suggest more than one individual, but the preservation and spatial distribution of the teeth might indicate otherwise (Fig. 1). The teeth with their inferred serial position, area of occurrence, and dimensions are listed in Table 1.

TABLE 1. Measurements of *P. oscillans* teeth, Henschke Fossil Cave.

Tooth	Specimen No.	Excavation area/level	length	ant. width	post. width
rM_1	P22736	A7/9	8.9	7.4	7.4
rM_2	P22734	A7/9	10.1	8.9	8.6
rM_3 or 4	P22815	A6/11	12.1	10.3	9.2
rM_3 or 4	P22826	A11 x /14 \pm †	10.7	9.3	8.7
II_1	P22816	A11 x /14 \pm †	36	n.a.	5.5
rP_3	P22733	A6/10	14.2	7.9	
IM_2	P17692	X3/3+	10.0	8.2	8.2
rM_3 or 4	P22814	A7/11	11.1	9.2	9.2
IM_2	P22735	A7/9	11.2	9.5	8.7
rM_3	P22813	A10/12	11.1	9.3	8.4

Measurements in mm. * approximate. † Specimen found during cleanup of slumped sediment from a large area centred on A11, previously excavated to level 17. Levels excavated were 15 cm thick except in this instance.

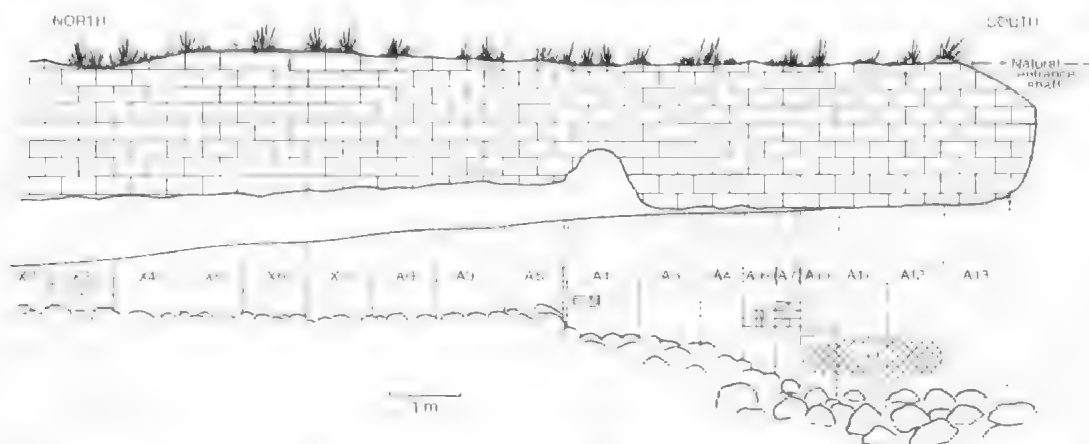


Fig. 1. Cross-section of deposit, Henschke Fossil Cave, Naracoorte, showing distribution of fossil *Propleopus* teeth. (Table 2.) C-14 in A1 indicates projected position of dated charcoal sample SUA-140 (>35 000 years B.P. δC^{13} -997.7 ± 4.0).

The cheek-teeth of *Propleopus* have been described adequately by Woods (1960), Bartholomai (1972) and Archer *et al.* (1978), and will be discussed here only in general terms. One of the notable features about the teeth is the very slight difference in characters that distinguish upper from lower, and indeed left from right, molars. They have roughly the same proportions in both upper and lower molars, and differ only in minute features such as a small lingual ridge coming forwards from the hypocone and a broad anterior cingulum on upper teeth, both absent on lower molars. These teeth bear a superficial resemblance to the deciduous molar M^1 of some short-faced kangaroos, *Sthenurus* spp. (*sensu lato*), in which the lophs are not as well-developed as in M^{2-5} . However, they are distinguished by different development of the midlink (mainly on the proto-loph in *Sthenurus*) and of the crest joining the paracone and metacone (straight and more vertical in *P. oscillans*). The M^1 of *Sthenurus* is also less rectangular than are the molars of *P. oscillans*.

One tooth (P22736) is considered here to represent an M^1 of *Propleopus*. This tooth is quadritubercular, almost rectangular and slightly longer than wide. It resembles the other molars in general form, but is smaller and relatively shorter, and cannot be matched with any described tooth. To some extent it also resembles upper molars (e.g. M^2 and M^3) of the Koala, *Phascolarctos cinereus*, which differ in being selenodont and less rectangular.

While the molar teeth of *P. oscillans* are all similar (Fig. 2), it has been possible to identify two of them with some certainty as last lower molars (M_3) by the reduced size of the talonid, the posterior half of the lower molar (Woods 1960). This is a feature of many marsupials. It was thus possible to check whether this tooth (P22736) was the last upper molar (M^3) of *P. oscillans* by testing the occlusion between it and the lower molars. There was, in fact, no possible match, because of the great size discrepancy. I therefore rule out the possibility that the tooth P22736 is a barely erupted M^3 , which tooth is yet unknown.

The specimen consists only of the enamel crown of the tooth, and is slightly worn on the cusps and crests. In the Henschke Fossil Cave this sort of preservation is typical of deciduous teeth, and those barely erupted teeth of juvenile individuals where the roots

and dentine apparently have not been fully calcified, allowing them to rot away.

I conclude that the tooth is an M^1 , despite the fact that it differs so greatly from the M^1 of *Hypsiprymnodon* (Ride 1961), which is a rather irregular three-cusped tooth with a poorly developed hypocone. This may imply a greater systematic separation from *Hypsiprymnodon* than is currently accepted (e.g. Bartholomai 1972). The condition of the tooth is much more like that of M^1 in *Bettongia*, where it is small and somewhat triangular but definitely quadri-tubercular. This agrees with the observations of Bartholomai (1972) on the permanent molars of *Propleopus*.

One of the major problems of "cave palaeontology" is the ever present risk of re-working of the fossils as they are moved piecemeal from the entrance to their final resting place. Some of the dangers are described by Archer (1974). In the present case, despite the considerable lateral and vertical distribution of the specimens, there is no real evidence for more than one individual and, if P22736 is an M^1 , the animal was a juvenile. This favours the interpretation that P22816 is a lower incisor of a juvenile *P. oscillans* and explains the difference from the only figured specimen (in OM F3302). Woods (1960) and Bartholomai (1972) have remarked upon the unique pattern of wear of *h.* This is not readily evident in P22816 due to its youth, but a similar wear profile (especially at the tip) may be seen and the enamel pattern corresponds in its ventrolateral distribution to that in *P. oscillans* (Woods 1960). The enamel is broken off short with the tooth, and staining indicates that only half the specimen was exposed in the jaw. These features and the tapering form of the tooth (which is smaller in both diameters than F3302) suggest that it undergoes considerable open-rooted growth during ontogeny.

Dimensions of known specimens of *Propleopus* teeth are given in Table 2. While the Naracorte teeth (Table 2) are slightly longer and narrower, where comparable, they clearly fit the proportions and description of *P. oscillans* better than *P. chillagoensis*.

The natural history of *Propleopus*

The teeth, jaw fragments, and associated fossils in the same deposits provide circumstantial evidence for interpretation of aspects of the habitat, as well as the ecological role of the animal within the habitat.

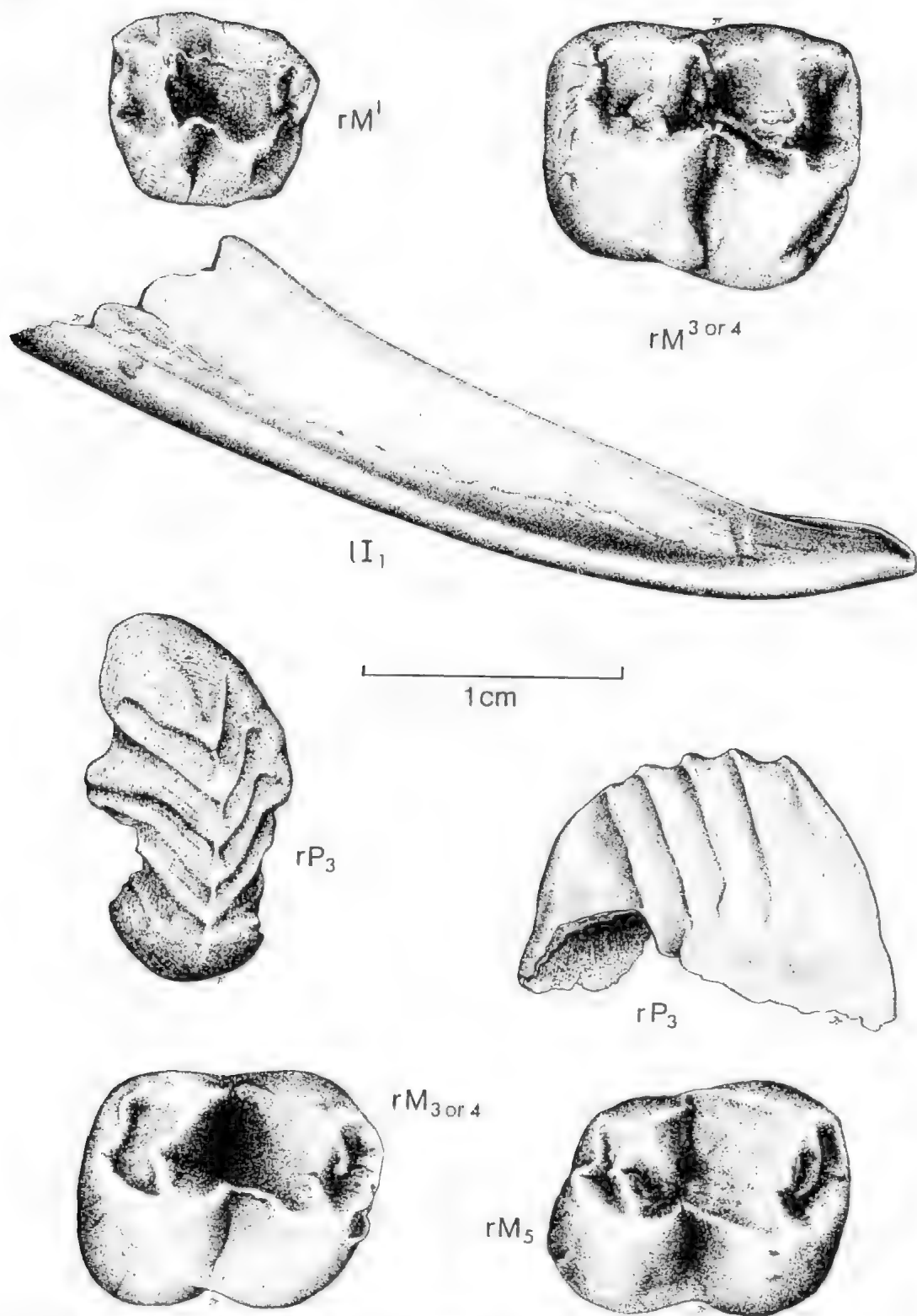


Fig. 2. Isolated teeth of *P. oscillans*, Henschke Fossil Cave, Naracoorte.

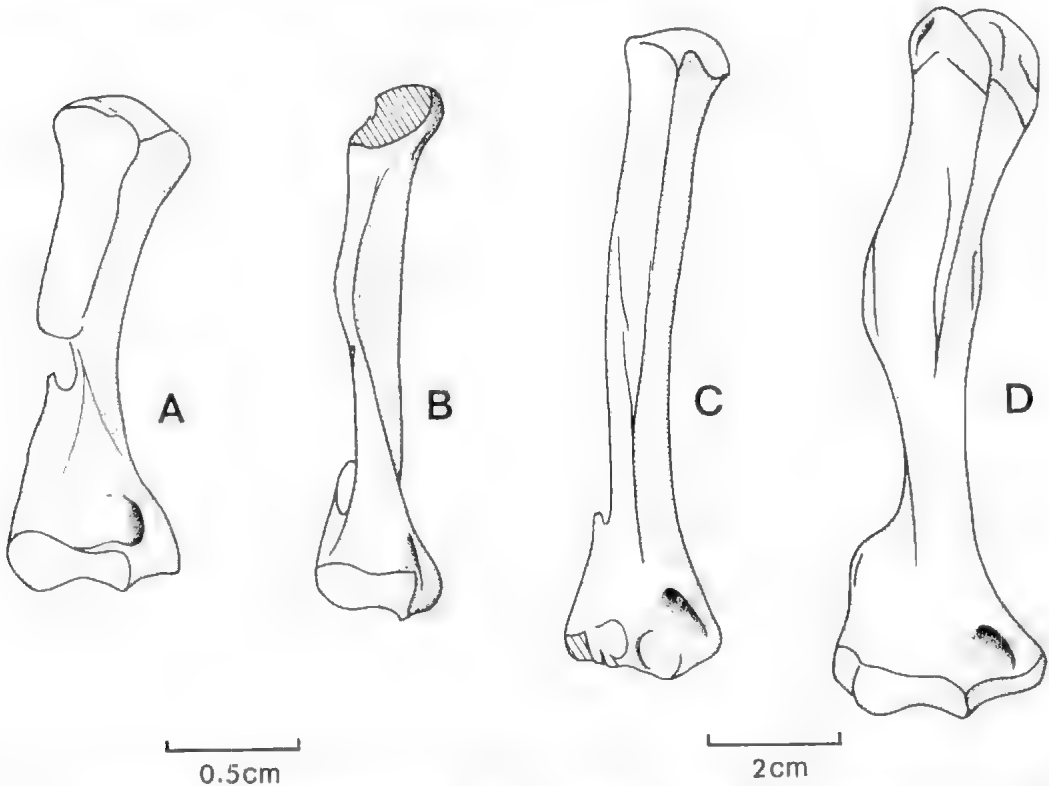
TABLE 2. *Propleopus* spp. tooth measurements (in mm), length x width (anterior/posterior)

Tooth	QM F6675 <i>P. oscillans</i>	NMV P15917 <i>P. chillagoensis</i>
P ³	15.2 x 10.8	21.1 x 13.0
M ²	10.5 x 9.7	9.7 x 12.5/10.9
M ³	11.1 x 10.3	9.7 x 11.0/ 9.6
M ⁴	—	10.2 x 9.5/ 7.6
M ³	—	9.3 x 7.5

	QM F3302 <i>P. oscillans</i>	UCMP 51697 <i>P. oscillans</i>	NMV P15919 <i>P. chillagoensis</i>	UCMP 45171 <i>Propleopus</i> sp.	SAM P20815 <i>P. oscillans</i>	SAM P22425 <i>P. oscillans</i>
I ₁	22.9 x 6.9	—	21.1 x 13.4	—	left	right
P ₁	13.9 x 9.7	*14 x 10	—	—	13.8 x 9.8	14.4 x 10.2
M ₂	9.5 x 8.7	* 9 x 9.5	—	9.6 x 9.7	10.0 x 8.9/ 9.1	9.8 x 9.1/ 9.2
M ₃	10.8 x 9.8	*11 x 9.5	—	10.2 x 10.6	11.1 x 10.3/10.2	11.3 x 10 /10.3
M ₄	11.2 x 10.3	*11 x 10	—	10.6 x 10.7	12.2 x 11.2/10.4	12.0 x 11.5/10.6
M ₅	11.0 x 9.6	—	—	10.1 x 9.0	11.2 x 10.1/ 8.5	11.6 x 9.9/ 8.6

* approximate, measured from Tedford (1967, Fig. 5.).

† approximate, damaged or in alveolo. (D. L. G. Williams pers. comm. 1980.)

Fig. 3. Comparison of macropodoid right humeri in anterior aspect. A: *Bettongia penicillata*, B: *Hypsiprymnodon moschatus*, C: cf. *Propleopus*, D: *Simosthenurus maddocki*.

1. *Size*: The molar teeth are as large as those of the Eastern Grey and Red Kangaroos, *Macropus giganteus* and *Megaleia rufa*. The only described lower jaw (the holotype) is also as large. I assume that *P. oscillans* had roughly the same bulk as the large kangaroos

(Woods 1960). In body proportions and build, however, it differed. The jaw is robust and similar in shape to those of *H. moschatus* and *Bettongia* (Woods 1960) rather than *Potorous*. In view of the apparent close relationship of *Propleopus* with *Hypsiprymnodon*,

we may assume they also had similar body proportions. *H. moschatus* differs from the potorines in having relatively long forelimbs (Woods 1960), apparently a primitive feature retained because of some advantage in its dense brush habitat. This difference in form from the other rat kangaroos is well shown in Troughton (1973, pl. XI). I calculated the approximate limb-bone ratios for *H. moschatus*, using the specimen QM JM2799, as follows:

humerus : radius : femur : tibia = 1 : 1.17 : 1.57 : 1.72. This compares with 1 : 1.19 : 2.3 : 2.78 for *Bettongia penicillata* Gray, 1837; 1 : 1.33 : 1.9 : 3.07 for the Western Grey Kangaroo *Macropus fuliginosus* (Desmarest); and 1 : 1.24 : 1.48 : 2.09 for the extinct short-faced kangaroo, *Simosthenurus madlocki* Wells & Murray, 1979. (SAM P17471-82) all of which are, or were, inhabitants of thick scrub. Only *M. fuliginosus* is a grazer, coming out into grassy clearings to feed.

In the Henschke Fossil Cave material there is a large humerus. It is straighter, more slender and more cylindrical than that of the kangaroos and potorines, and it has markedly reduced deltoid and pectoral ridges and a shorter supinator crest. Of the marsupials compared with it (including species of *Bettongia*, *Hypsiprymnodon*, *Macropus*, *Sthenurus*, *Thylacinus*, *Thylacoleo*, *Phascogale*) the fossil bone most closely resembles the humerus of *H. moschatus*, but is even straighter and more cylindrical (Fig 3). The total length of the fossil humerus is estimated at 195 mm. Assuming that it represents *P. oscellans*, and applying the *Hypsiprymnodon* ratios, the radius length is 228 mm, femur 306 mm, and tibia 335 mm; measurements indicating an animal as bulky as a grey kangaroo but with shorter hind legs and much longer fore-legs.

2. *Food*: The teeth are relatively simple in form, quadritubercular and bunodont. These features are also typical of mammals such as Man, pigs and bears, all of which have an omnivorous or browsing vegetarian diet, as in fact have living potoroids. Hume (1978) considered *H. moschatus* to be omnivorous, and Ramsay (1876) recorded that it eats "... insects, worms and tuberous roots ..." and palm berries (*Archontophoenix* (*Ptychosperma*) *alexandrae*). The retention of relatively long forelegs may reflect its method of

food gathering, namely turning over scrub debris, and digging like a bandicoot (Troughton 1973). The large secant premolars also seem connected with an omnivorous diet, possibly being used to cut flesh as well as vegetable matter. *P. oscellans* probably lived on soft herbaceous vegetation, carrion, invertebrates, and meal.

3. *Habitat*: *Hypsiprymnodon* and some of the other potoroids live in dense wet scrub where they can obtain protection against predators. Although so much larger than the living rat-kangaroos, *Propleopus* may have had the same need. Its presumed stocky build would be an advantage in thick brush, just as it seems to be to the stocky Kangaroo Island kangaroo (*M. f. fuliginosus*). The associated fauna adds some support to the idea. Although there are a few fossils species present (such as *Lasiornis* sp. and *Procoptodon* sp.) that might suggest a more open environment, the abundance of brush-dwelling animals, such as potorines, small wallabies (mainly *Macropus rufogriseus*) and bandicoots, indicates the presence of moderately shrubby, open forest in the Naracoorte area during the late Pleistocene. The browsing short-faced kangaroos (*Simosthenurus* spp.) are common and the cow-sized diprotodontid *Zygomaturus trilobus* also is present: these are believed to have inhabited moderately thick scrub. *Diprotodon opalum*, which I consider to be an open scrub or plains animal, is rare; only fragments of three teeth have been recognized. Tortoises (*Chelonia* cf. *longicollis*) were abundant in a nearby swamp. The overall picture given by the fossil fauna is of an area at Naracoorte more thickly forested and with heavier scrub or thicker understory, and a higher rainfall than today.

Thus *Propleopus* may be seen as a large, bulky, relatively short-legged animal, living in dense thickets and scrub, and eating succulent herbaceous vegetation, insects and other small animals and possibly carrion. Its rarity in the fossil record may reflect its strong preference for thick scrub, where remains seldom become fossilized. It may be significant that the fossils reported here represent a juvenile individual, one that was perhaps less cautious than an adult.

Acknowledgements

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Creek specimen. Dr J. K. Ling and Mr P. F. Aitken gave constructive criticism of the manuscript, which was typed by Mrs Joan Murphy. Jenni Thurmer drew the figures.

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STRUCTURE AND FUNCTION OF THE TIBIAL GLAND OF THE AUSTRALIAN FROG LIMNODYNASTES DUMERILI PETERS

BY G. A. CROOK & M. J. TYLER

Summary

Limnodynastes dumerili has a large, oval, dermal gland on the tibia; it is perforated with ducts at a density of 6/mm². In horizontal section the gland appears as a series of large horizontal chambers filled with secretions. The ontogeny of glands in tadpoles is described.

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Summary

G. A. CROOK & M. J. TYLER (1981) Structure and function of the tibial gland of the Australian frog *Limnodynastes dumerili* Peters. *Trans. R. Soc. S. Aust.* **105**(2), 49-52. 12 June, 1981.

Limnodynastes dumerili has a large, oval, dermal gland on the tibia: it is perforated with ducts at a density of 6/mm². In horizontal section the gland appears as a series of large horizontal chambers filled with secretions. The ontogeny of glands in tadpoles is described.

When the gland secretion is expressed manually to the surface, rats avoid the frog. In the absence of expression the frog is eaten but the glands are left untouched. Predators of the frog and closely related species with similar glands are listed.

Introduction

In the Anura there are diverse kinds of discrete dermal glands. Examples are the parotoid glands of many species of *Bufo* (Blair 1972); the dorsal lipid glands of South American phyllomedusine hylids (Blaylock *et al.* 1976); the supralabial glands of *Rana* (Smith 1954) and the tibial glands of some species of *Bufo* (Blair 1972) and some Australian frogs of the genus *Limnodynastes* (Martin 1972; Tyler 1976).

Much attention has been devoted to parotoid glands and their secretions (Low 1972): the structure and possible functions of the tibial glands have not been examined. Here we describe the gross structure and ontogeny of these structures in the southern Australian species *Limnodynastes dumerili*, and investigate their possible role.

Limnodynastes dumerili is a robust species measuring up to 75 mm snout to vent length when fully grown. It is widely distributed in southeastern Australia and is a member of the *L. dorsalis* group of species, whose representatives extend over the eastern and south-western portions of the continent (Martin 1972). Illustrations of the frog appear in Barker & Grigg (1977), Tyler (1977, 1978) and Cogger (1979).

Material and methods

The specimens used in this study were collected at various localities within an 80 km radius of Adelaide and were maintained for varying periods in vivaria in the University of Adelaide.

Glands were obtained from freshly decerebrated and spinalised animals. They were dissected free from the tibia and for histological preparations were fixed in 10% buffered formalin. Sections were cut at 7 μ m and stained with haematoxylin and eosin. For studies where glands were exposed to potential predators, minimal time elapsed between the death of the donor and such exposure. In six trials, groups of four rats were fasted for 48 hours and the entire dead frog offered, the entire frog minus the glands, or gland secretions wiped upon the surface of rat pellets or fresh meat.

Studies of ontogeny were based on tadpoles collected at stages 25-32 of Limbaugh & Volpe (1957) and reared on a diet of boiled lettuce leaves. Samples were taken from this stock at intervals determined by hindlimb development.

Gross and histological structure

The tibial glands of *Limnodynastes dumerili* are single, raised, ovoid, dermal structures on the dorsal surface of each tibia and occupying more than 50% of the dorsal aspect of that limb segment (Fig. 1). Dimensions of the gland in a 75 mm frog are 15 x 11 mm. In a series of nine specimens the length of the gland was 51-69% of the length of the tibia. The gland is entirely dermal and does not adhere to underlying muscles. It is palpable and resilient. The dorsal surface of the gland is perforated by the apertures of numerous ducts at a frequency of approximately 6/mm². In some frogs the gland is pigmented with a metallic sheen contrasting with the remainder of the dorsal skin, however in the majority there was no such colour differentiation.

In transverse section (Fig. 3) the gland has a regular, columnar arrangement of cavities

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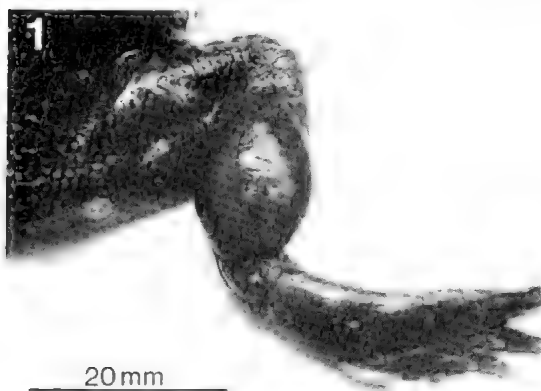


Fig. 1. Dorsal aspect of right hindleg of *Limnodynastes dumerili* showing large, protuberant tibial gland.

filled with vast quantities of secretion, and communicating to the exterior via short, narrow ducts. The stratum corneum is of moderate thickness, and mucus glands are comparable in size with those of other frog species. In horizontal section (Fig. 2) the regular shape and repetitive form of the secretory cavities is revealed. In the illustration the secretory contents have contracted from the very narrow matrix of connective tissue. We attribute this to the dehydration process during histological preparation. At higher magnifications a few small, circular vesicles could be detected within the secretory material.

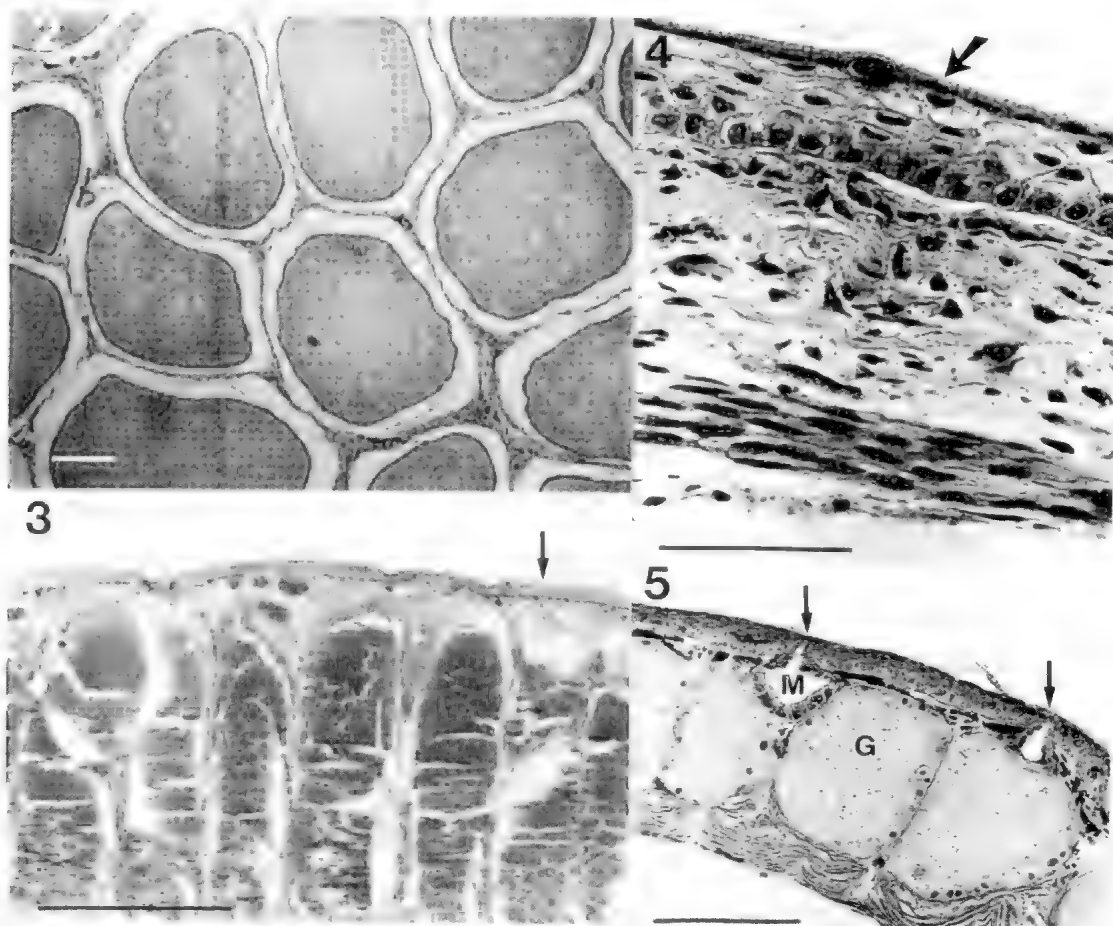


Fig. 2. Horizontal section of tibial gland. Dense areas are the internal secretions of the gland. These secretions have contracted slightly. Scale bar = 100 μ m. Fig. 3. Transverse section of portion of tibial gland. Note columnar arrangement of the internal matrix, and duct (arrowed). The smear of secretions in the gland is fractured as a result of histological preparation. Scale bar = 1 mm. Fig. 4. Transverse section of skin of tibial region of tadpole at stage 39 of Limbaugh & Volpe (1957). Note occurrence of cell nuclei in most superficial portion of stratum corneum (arrowed). Scale bar = 50 μ m. Fig. 5. Transverse section of skin of tibial region of tadpole at stage 43 of Limbaugh & Volpe (1957). Granular glands (G) and mucus glands (M) are well developed and communicate with the surface via open ducts (arrowed). Scale bar = 100 μ m.

The gland is innervated by a branch of the sciatic nerve, and there is a network of blood vessels upon the ventral surface of the gland.

The tibial glands first become evident in the tadpole at stage 42 and become more prominent until, at stage 46, they assume the oval form characteristic of those of the adult. At stage 39, the general adult structure of the skin is recognizable (Fig. 4), but the second layer of the stratum corneum contains cells with nuclei whereas in the adult no nuclei occur there. The stratum spongiosum is very thin and non-glandular. Glands are represented in the epidermis by aggregations of cells.

At stage 40 the ultimate layering of skin is distinguishable. Glands are present in the stratum spongiosum and some have formed lumina. The evidence suggests that the glands develop downwards into the stratum spongiosum, and continue to enlarge there. By stage 41 the lumina of the granular glands are fully formed and secretion by the now comparatively thin inner layer of epithelial cells has begun. The secretion is in the form of spherical globules. Ducts connect the glands to the surface. The epidermis has changed and assumed the adult form with enucleate stratum corneum cell layers. Aggregations of epidermal cells represent incipient mucus glands. By stage 43 the mucus glands have developed lumina containing mucus. The granular glands have expanded to occupy nearly the entire stratum spongiosum (Fig. 5).

At stage 44 granular glands in the tibial gland are in various developmental states. The glands at the centre have expanded to occupy the entire stratum spongiosum and are very tightly packed together. However, the peripheral ones are small and less dense. By stage 45 the mucus glands are well developed and the granular glands occupy the entire stratum spongiosum. At stage 46 the granular glands have increased further in area and the stratum spongiosum has expanded to accommodate them. The glands are tightly packed and thus comparable with the form of the adult tibial gland.

Function of tibial glands

Because the tibial gland appears during late larval life, it is clearly of functional significance only to the adult. The potential range of functions is extensive, but protection from predators appeared the most fruitful direction of investigation. Examination of the literature established that *L. dumerili* and its close relatives sharing tibial glands are normally eaten by a wide variety of vertebrates (Table 1).

We fed freshly killed frogs to several vertebrate predators: *Chelodina longicollis*, Freshwater Tortoise, ate tadpoles and juvenile frogs with no adverse effects; *Notechis scutatus*, Tiger Snake (no effect upon the snake); *Anas platyrhynchos*, Mallard (juveniles up to 40 mm in length eaten readily) and also to *Rattus norvegicus*, rat. Rats ate every portion

TABLE 1. Predation upon frogs of the *Limnodynastes dorsalis* species group

Species of frog	Predator	Details	Source
<i>L. dorsalis</i> *	<i>Vulpes vulpes</i> (Red Fox)	In 1% of stomachs investigated, 1958 In 7.7% of stomachs investigated, 1959	McIntosh 1963
<i>L. dumerili</i> †	<i>V. vulpes</i> (Red Fox)	1 in stomach	J. D. Croft (pers. comm.)
<i>L. dumerili</i> ‡	<i>Notechis scutatus</i> (Tiger Snake) <i>Pseudechis porphyriacus</i> (Black Snake)	Fed to captive specimens	E. Worrell (pers. comm.)
<i>L. dumerili</i>	<i>Litoria raniformis</i> (frog)	Observed swallowing <i>L. dumerili</i> on two occasions. Predator unaffected	M. J. Tyler (unpublished)
<i>L. dumerili</i>	Owls	Bones of numerous frogs found in regurgitated owl pellets	M. J. Tyler (unpublished)

* Frog species identified as "*L. dorsalis*" were reclassified as a complex of species by Martin (1972).

† Identity uncertain; captured in areas of sympatry between *L. dumerili* and *L. terraereginae*.

‡ Identity uncertain; locality data unknown.

of the frog except the tibial glands and a small strip of skin joining the glands together. The experiment was performed six times with the same results: namely that rats fasted for 48 hours would eat the entire *L. dumerili* with the sole exception of the tibial glands. However in the experiments in which exudate from the glands was expressed onto the outer surface of the skin, the fasted rats would not eat any part of the frog. Having appeared to taste the gland's contents they exhibited great distress, running around the cage, and making wiping motions with their paws. However, when the tibial glands were removed from the frog, the rats ate the hind limbs with the rest of the body.

When food objects were coated with the secretion and offered to fasted rats, the items were rejected after initial investigation (usually by licking, and this activity was followed by extensive cleaning of the mouths and paws).

Discussion

We have not performed pharmacological or biochemical investigations to determine the identity of the glandular secretion, but we note

that in their survey of pharmacologically active substances from the skin of Australian frogs, Roseghini *et al.* (1976) reported that in the *L. dorsalis* group a variety of substances widely distributed in other species was absent, with the exception of 5-Hydroxytryptamine (5-7 $\mu\text{g/g}$ skin). Although we are unable to identify the substance involved, our observations indicate that the secretions of the tibial glands afford the animal a degree of potential protection from at least some of the animals likely to predate upon it if the secretions are released from the glands. However the efficacy of the mechanism is uncertain. The secretions can be expressed by applying lateral pressure to the glands, but we have failed to observe release under other forms of stress.

Acknowledgments

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BENNELONGIA, A NEW CYPRIDIDID OSTRACOD GENUS FROM AUSTRALASIA

BY P. DE DECKKER & K. G. MCKENZIE

Summary

A new Australian ostracod genus and species *Bennelongia harpago* (Family: Cyprididae Baird, 1843) is described from Queensland.

BENNELONGIA, A NEW CYPRIDIDID OSTRACOD GENUS FROM AUSTRALASIA

by P. DE DECKKER* & K. G. MCKENZIE†

Summary

DE DECKKER, P. & MCKENZIE, K. G. (1981) *Bennelongia*, a new cypridid ostracod genus from Australasia. *Trans. R. Soc. S. Aust.* **105**(2), 53-58, 12 June, 1981.

A new Australian ostracod genus and species *Bennelongia harpago* (Family: Cyprididae Baird, 1843) is described from Queensland.

Introduction

The ostracod *Chlamydotheca australis* Brady, 1886 was described from empty shells collected at Penola, South Australia. Sars (1894) synonymized *C. australis* with *Cypris bennelong* King, 1855 after examination of New Zealand specimens but Müller (1912) queried their congeneric status. Henry (1923) followed Sars' (1894) concept of the synonymy and Chapman (1967) later transferred the species to *Cyprinotus*.

McKenzie (1971) in his review of the palaeozoogeography of freshwater Ostracoda, referred to the above species as the "*Chlamydotheca australis* species group", and pointed out anatomical differences between this group and *Cypris* and *Chlamydotheca* s.s. This therefore indirectly suggested the need to erect a new genus to include the Australian and New Zealand species.

Since a collection of ostracods from Queensland, made available to both authors by Mr C. Bentley, yielded a new species belonging to the new genus, it was decided to describe it jointly, and it is here referred to as *Bennelongia harpago* n.gen., n.sp.

Systematic description

Family CYPRIDIDAE Baird, 1845

Subfamily CYPRIDINAE Baird, 1845

Bennelongia n.gen.

Type species: *Bennelongia harpago* n.sp.

Bennelongia n.gen.

Diagnosis: Adult with strongly asymmetrical valves anteriorly: left valve beak-like anteroventrally; selvaige displaced inwards with

inner list forming broad but short lip-like structure which does not extend anterodorsally. Anteroventral area of right valve usually smooth-curved but occasionally with beak-like flange. Juvenile with symmetrical valves and no beak-like structure; external surface either deeply pitted or reticulated, often with many wart-like tubercles.

Asymmetrical male maxillary palps; thoracopoda 1st segment with two unequal setae and penultimate segment weakly divided; lateral lobe of hemipenis broadly boot-shaped.

Derivation of name: From *Bennelong*, the first aboriginal to have a long association with the early European settlers of Australia.

Discussion: McKenzie (1971) noted anatomical differences between the new genus and the genera *Cypris* O. F. Müller, 1776, *Chlamydotheca* Saussure, 1858, *Riocypris* Klie, 1935 and *Globocypris* Klie, 1939. A unique feature of the shell distinguishing *Bennelongia* from the otherwise similar South African Cypridinae, is the broad but short lip-like inner list which does not extend anterodorsally.

Bennelongia australis (Brady) and congeners are described in De Deckker (1981).

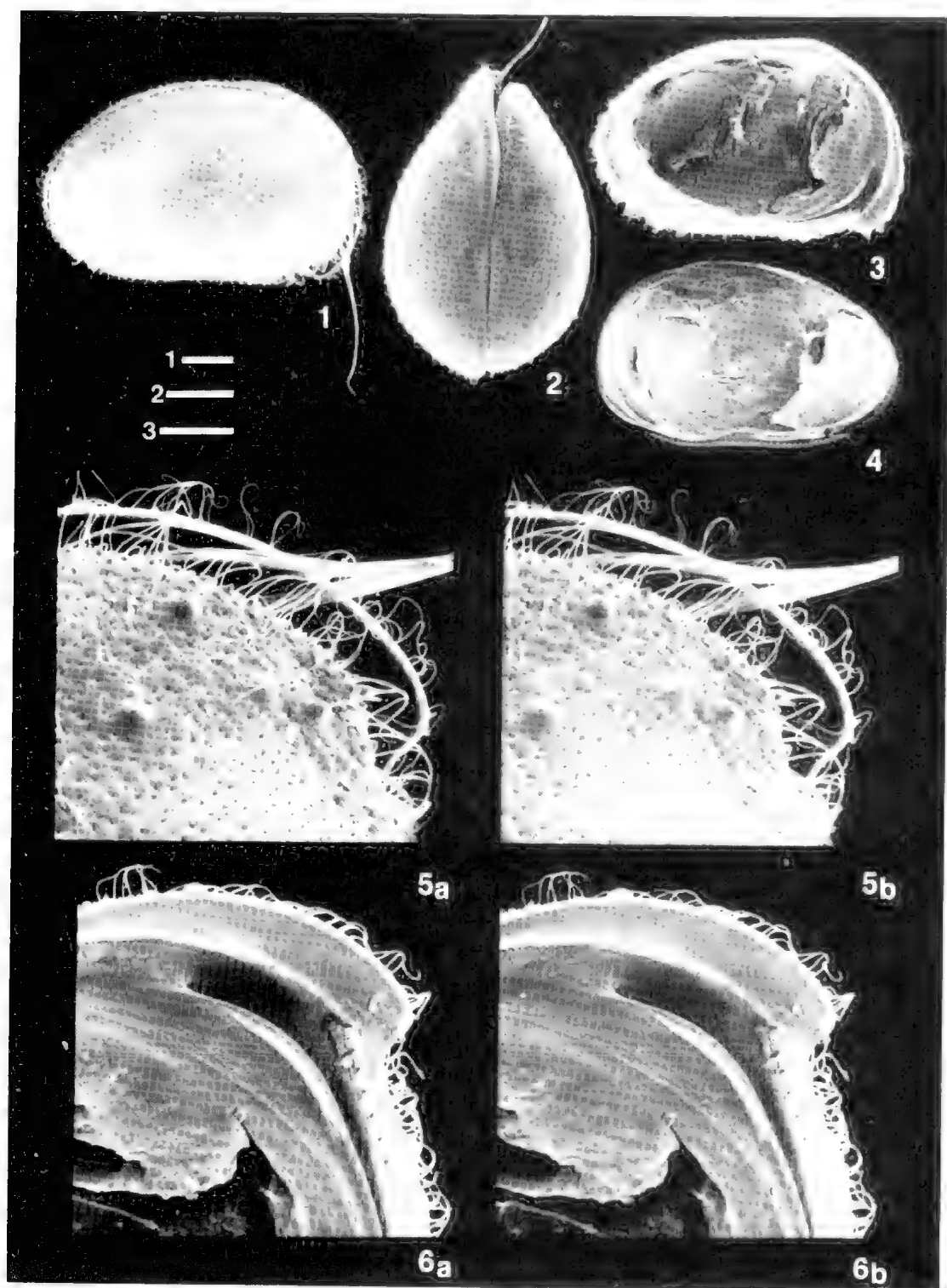
Bennelongia harpago n.sp.

FIGS 1-19

Description: Carapace (external) oval to subrectangular in lateral view; oval in dorsal view. Greatest height at about 1/3 from anterior where dorsal thickening of shell forms overlap in larger left valve. Valves asymmetrical; anteroventrally, left valve "beak"-shaped and extends much further than right valve which is broadly rounded in that area. Deep concavity just posterior to "beak"-like feature of left valve, whereas mouth region only slightly inflexed in both valves. Left valve overlaps other in anterior region of hinge, posteriorly, and ventrally where overlap is broadest. Shell

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Figs 1-6. *Bennelongia harpago* n.gen., n.sp. 1. Lateral view of carapace showing RV of paratype, P31613. 2. Dorsal view of carapace of paratype P31614. 3. LV internal of holotype, P31612. 4. RV internal of holotype, P31612. Fig. 5 a-b Detail of anterior area of Fig. 1 (stereo pair). Fig. 6 a-b Detail of anterior area of Fig. 3 (stereo pair). Scale 1 = 150 μ for Figs 1-4, 2 = 50 μ for Figs 5 a-b, 3 = 100 μ for Figs 6 a-b. LV, RV = left valve, right valve.



Figs 7. *Remelonia harpago* n.gen., n.sp. Internal view of LV paratype, P31615.

pseudopunctate with simple rimmed type normal pore canals and with number of broad pustules anteriorly and posteriorly, some of which are perforated by normal pores. Periphery of right valve tuberculate along ventral margin.

(Internal) Inner lamella broader anteriorly and broadest in left valve. Inner list develops into broad lip anteroventrally in left valve in "beak" region and absent anterodorsally; in front of lip is a deep groove; selvage nearly peripheral in posterior region. In right valve, inner list narrow and nearly peripheral all round except anteroventrally where it is broader; anteriorly, groove runs parallel to it. Selvage tuberculate ventrally. Anteriorly, radial pore canals long, numerous and straight. Adductor scars consist of two rows of three scars, anterior scars being slightly broader; an additional small scar behind and below bottom scar of front row, and anterior to and below posterior row. The two mandibular scars long and narrow.

Anatomy: Antennula: (Fig. 8) 7-segmented; length-width ration of last six segments:

$$\frac{3.4}{2}, \frac{2.1}{3}, \frac{1}{1}, \frac{1}{1.4}, \frac{0.7}{1}, \frac{1}{3}.$$

Natatory setae slightly longer than all segments together. Penultimate segment with one small bristle and four natatory setae and distal segment with three natatory setae. For placement of other setae and bristles see Fig. 8.

Antenna: (Fig. 13) with four claws: three equal ones all slightly pectinate on penultimate segment plus additional claw on last segment reaching tip of other three. Distal segment with additional short, slim pectinate claw. Natatory setae reaching tips of claws.

Mandible: (Fig. 12) epipod with five long and plumose Strahlen and a smaller one on side of plate; coxale with seven teeth; endopod with α bristle long, narrow and smooth, β bristle short, stout and tufted all over, γ bristle almost twice length of distal segment, and pilose in distal half.

Labrum: For detail see Fig. 9.

Rake-like organ: (Fig. 17) five teeth and additional bifid one on inner side of each rake.

Maxillula: (Fig. 15) epipod with 17 Strahlen and four downwards pointing setae; 3rd lobe with two smooth Zahnborsten; length

ratio of palp segments $\frac{2.8}{1}$; distal segment

of palp rectangular.

Maxilla: (Fig. 11) endopod with three terminal bristles, one short and two others of almost equal length and slightly more than twice length of short one; epipod with five plumose Strahlen. For chaetotaxy of protopodite, see Fig. 11.

Thoracopoda I: (Fig. 14) protopod coxa with one long dorsodistal bristle, geniculate basis with one long bristle; 2nd segment with one long inner distal bristle; penultimate segment divided and bearing long inner bristle at mid-length where it is divided and two unequal inner bristles distally; distal segment with two short distal bristles, one on inner side and other on outer side. Claw long and pectinate.

Thoracopoda II: (Fig. 18) terminal segment with two unequal bristles: short one hook-shaped and half length of other.

Furca: (Fig. 16) claws unequal; anterior one 1.4 x length of other; anterior bristle half length of posterior one which is $\frac{2}{3}$ length of small claw.

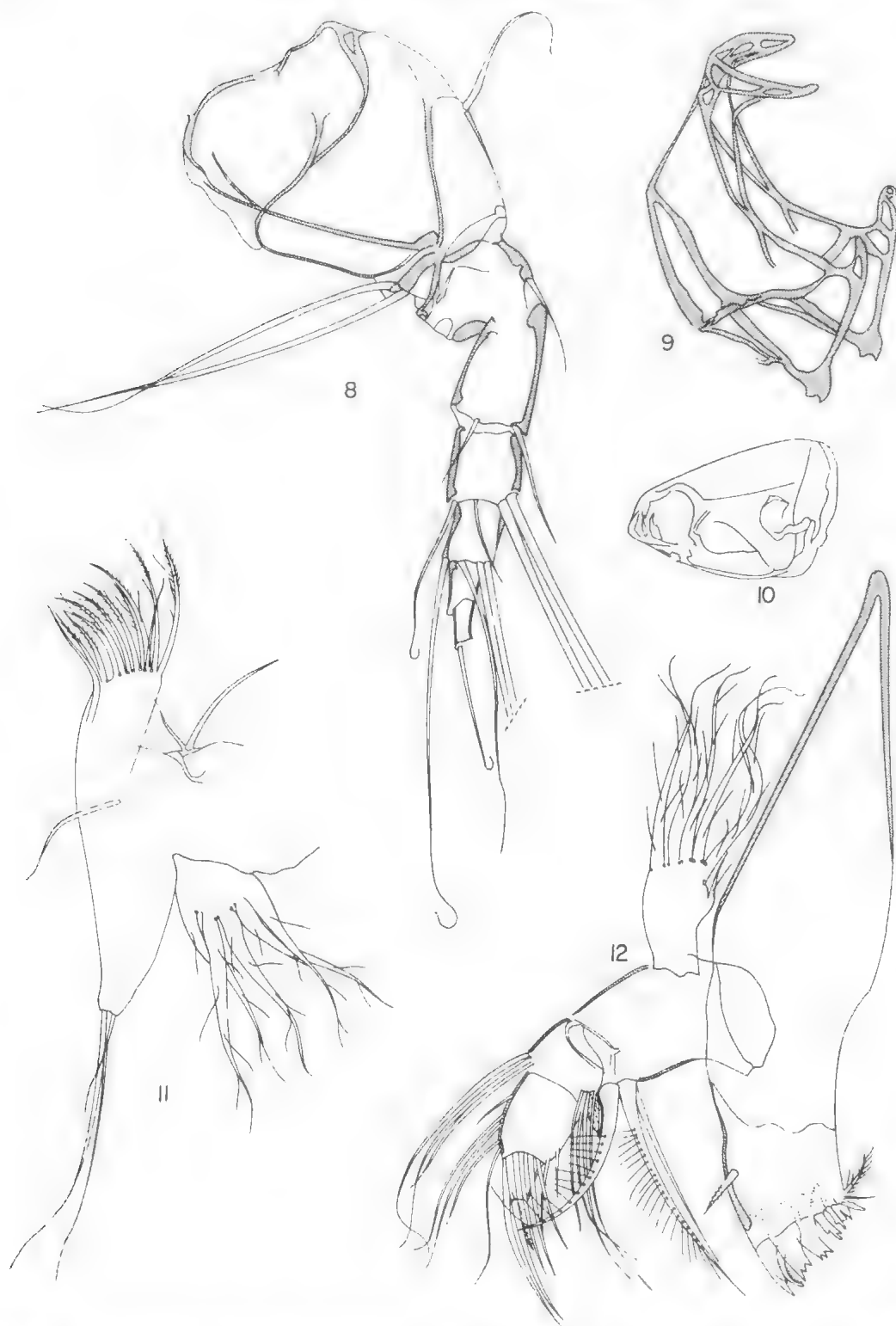
Furcal attachment: (Fig. 19) median branch slightly curved; ventral and dorsal branches forming right angle and hook-shaped at tip.

Genitalia: weakly chitinous. For outline refer to Fig. 10.

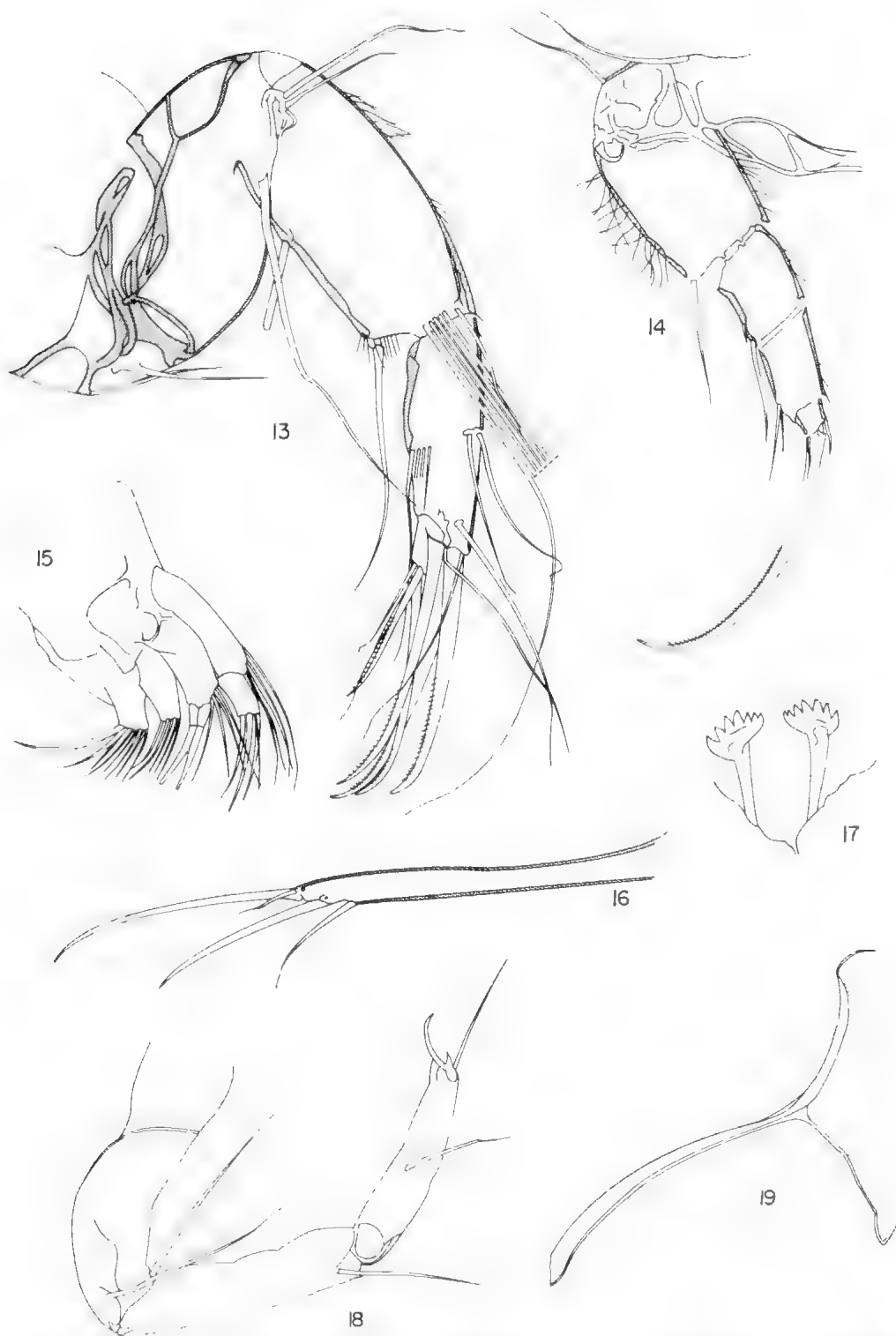
Colour of shell: green with beige strips in dorsal area.

		length	height
Size: holotype:	LV	1020 μ	600 μ
	PV	920 μ	580 μ

Holotype: AM P31612; Paratypes: AM P31613—P31615 (Australian Museum)



Figs 8-12. *Benneclongia harpago* n.gen., n.sp., holotype P31612. 8. Antennula; 9. Labrum; 10. Genitalia; 11. Maxilla; 12. Mandible; all x 150.



Figs. 13-19, *Bennelongia harpago* n.gen., n.sp., holotype, P 31612. 13. Antenna, 14. Thoracopoda I, 15. Maxillula—palps and lobes, 16. Furca, 17. Rake-like organs, 18. Thoracopoda II, 19. Furcal attachment. All x 150.

Type locality: Dam (19°16'18"S, 144°36'22"E) near Mt Teddy, beside McKinnons Creek, Lyndhurst Station, on the Kennedy Highway near Einasleigh, Queensland.

Distribution: *B. harpago* also has been collected at the following localities in Queensland: L. Powlathanga, near Charters Towers; Cauckingburra Swamp at L. Buchanan, near Charters Towers; roadside swamp at Calen; Farm Dam, Mingela.

Ecology: Found in fresh waters. At the type locality, it has been collected from the margin of the dam among aquatic plants at a depth

of about 30–45 cm. No males have been found.

Acknowledgements

We are grateful to Mr C. Bentley for the type material and Dr B. V. Timms for the other Queensland collections. We are thankful to Mrs R. Hughes who inked the original drawings, Mr P. G. Kempster for his help with the photography, and Ms C. Twang and Mrs J. Harden for the typing.

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EXCHANGE PROCESSES FOR UPPER SPENCER GULF, SOUTH AUSTRALIA

BY J. A. T. BYE

Summary

Upper Spencer Gulf, which is defined as lying north of Lowly Point in Spencer Gulf, South Australia, is characterised by a salinity regime in which there is an approximate equilibrium between a northward advection of salt by a small mean current of about 0.1 mm/s that is necessary to maintain the water level constant in the presence of the annual net evaporation, and a southward diffusion of salt, probably by the shear effect induced by strong tidal currents. These processes have been studied theoretically using diffusion coefficients determined from the available salinity and net evaporation data. Approximate agreement with the observed mean and annual variation of salinity is obtained for the reported diffusion coefficients if the actual evaporation rates for upper Spencer Gulf are about 0.5 that of the regional pan evaporation rates.

EXCHANGE PROCESSES FOR UPPER SPENCER GULF, SOUTH AUSTRALIA

by J. A. T. BYE*

Summary

BYE, J. A. T. (1981) Exchange processes for upper Spencer Gulf, South Australia, *Trans. R. Soc. S. Aust.* **105**(2), 59-66, 12 June, 1981.

Upper Spencer Gulf, which is defined as lying north of Lowly Point in Spencer Gulf, South Australia, is characterised by a salinity regime in which there is an approximate equilibrium between a northward advection of salt by a small mean current of about 0.1 mm/s that is necessary to maintain the water level constant in the presence of the annual net evaporation, and a southward diffusion of salt, probably by the shear effect induced by strong tidal currents. These processes have been studied theoretically using diffusion coefficients determined from the available salinity and net evaporation data. Approximate agreement with the observed mean and annual variation of salinity is obtained for the reported diffusion coefficients if the actual evaporation rates for upper Spencer Gulf are about 0.5 that of the regional pan evaporation rates.

The response time scale for a dissolved substance is a function of the departure from equilibrium of its concentration, and for the annual salinity cycle, the time scale is about 300 days. Substances introduced into upper Spencer Gulf at approximately its midpoint would have a residence time of about 180 days, and transient injections would initially disperse on a time scale about 120 days, but this time scale would increase as the remnant concentration of substance declines.

A higher pan factor with proportionately higher diffusion coefficients would also approximately reproduce the observed salinity patterns, and for a pan factor of 0.67 (as reported for Lake Eyre) the dispersion times would be reduced by about 25%. This figure is the suggested overall accuracy for the predictions.

Introduction

Upper Spencer Gulf may be defined as that part of Spencer Gulf to the north of Lowly Point. It contains a water volume of approximately 4 km³, and has a surface water area of about 500 km², and a length of about 65 km (Fig. 1). Below Lowly Point, Spencer Gulf increases markedly in width, and this region appears as a transition region between a basically longitudinal hydrological regime, and the more general circulation patterns of lower Spencer Gulf (Bullock 1975). Indeed the longitudinal nature of upper Spencer Gulf allows methods of oceanographical analysis which are much simpler than in the general situation to be applied, and results on the exchange rates between upper and lower Spencer Gulf to be obtained.

Physical Principles

The dominant currents in upper Spencer Gulf are tidal currents (Radok 1978), which normally generate sufficient turbulent mixing in the vertical to cause dissolved substances to become almost uniformly distributed in the

water column. Thus the concentration patterns can be described basically using vertically averaged values. The observed salinity patterns now suggest that a further approximate

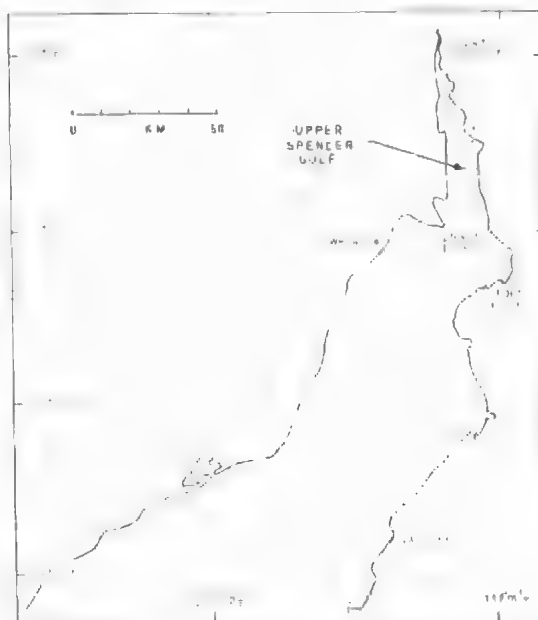


Fig. 1. Upper Spencer Gulf. x indicates location of sources.

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averaging may be taken for each cross-section of the gulf to yield an essentially longitudinal property distribution. An understanding of this simplified situation yielding information on exchange rates is readily obtained, and is presented in later sections. It should be noted however that there may be significant cross-sectional distributions associated with the inflow regions of substances introduced within upper Spencer Gulf, as distinct from sea salt which has no significant internal sources.

The turbulent motions induced by the tidal currents give rise to a longitudinal diffusion probably by a process known as the shear effect (Bowden 1965). The resulting coefficients of longitudinal diffusion are large, and tend to increase with water depth. Thus there is a mechanism that transports substances in the opposite direction to the mean concentration gradients within the gulf, i.e. southwards; this process is present independently of any mean water transport. In fact a steady-state concentration distribution occurs when the southward turbulent diffusion of substance is balanced by the northward advection induced by the flow into upper Spencer Gulf necessary to compensate for the water lost by the net evaporation at the surface. This balance is the key to the understanding of the mean salinity distribution, or indeed the average concentration pattern for any substance, including that with a source in upper Spencer Gulf.

Thus, measurements of the salinity distribution in upper Spencer Gulf together with the net evaporation rates enable calculations to be made of the diffusion coefficients, which in turn allow predictions to be made for the behaviour of any introduced substance. The theoretical formulation of these processes is given in the next section.

Theory

Consider a one-dimensional (longitudinal) distribution of substance along Ox , then its conservation equation (Nihoul 1975) has the form.

$$\frac{\partial}{\partial t} Ac + \frac{\partial}{\partial x} Qc - \frac{\partial}{\partial x} (KA \frac{\partial c}{\partial x}) = P/\rho$$

in which t is time, $Q(x,t)$ is the volume transport along Ox , $K(x)$ is the (local) coefficient of eddy diffusion, $A(x,t)$ is the cross-sectional area, $P(x,t)$ is the net rate of production of substance/unit length, $c(x,t)$ is

the concentration of substance, and ρ is a reference water density. The volume transport, Q , is given by the equation,

$$\frac{\partial Q}{\partial x} = -b \left(\frac{\partial \eta}{\partial t} + E - R \right)$$

where $b(x)$ is the breadth of the channel, $E(x,t)$ is the evaporation rate, $R(x,t)$ is the rainfall rate, and $\frac{\partial \eta}{\partial t}$ is the rate of change of water level. This pair of equations, together with the boundary conditions that the concentration is specified at the open end of the gulf (x_1) i.e.

$$c|_{x_1} = c_0(t)$$

and that the flux of substance, and the volume transport through the top end of the gulf (x_0) are zero, i.e.

$$KA \frac{\partial c}{\partial x} - Qc|_{x_0} = 0, \quad Q|_{x_0} = 0$$

is sufficient to determine solutions for $c(x,t)$.

It is assumed for simplicity that K is independent of time, and that $\frac{\partial \eta}{\partial t}$ is independent of distance. This latter condition is approximately valid for the progression of long period ($\gtrsim 1$ week) water level changes, mainly of meteorological origin, which are observed to propagate into the South Australian Sea. Changes in cross-sectional area with time for these waves are assumed to be given by the relation.

$$\frac{\partial A}{\partial t} = b \frac{\partial \eta}{\partial t}$$

The net rate of production, P , consists of two parts; a production rate, p , associated with the introduction of substance, and a decay rate which is due to (a) breakdown of the substance, d , and (b) exchange with the atmosphere or sediments, s . Thus,

$$P = p - d - s$$

where $d = \rho \lambda c$ and $s = \rho b_\mu c$

in which λ is a breakdown time constant, and μ is an exchange velocity with the atmosphere or sediments.

The method of solution of the equations uses a finite-difference representation with a resolution of 2 km, and extends over 180 km, approximately from the top of Spencer Gulf above Pt Augusta to Wallaroo. Solutions of the steady-state concentration equation for the same region have been discussed previously in Bye (1976).

Determination of the diffusion coefficients

For a steady-state distribution with $P = 0$, the pair of governing equations may be combined to yield the relation,

$$K(x) = - \frac{z(E - R)c}{A \frac{\partial c}{\partial x}}$$

where $z(x) = \int_{x_p}^x b dx$ is the surface area of the gulf to the north of x . On substituting for the quantities on the right hand side of the equation from observed salinity data, and estimated net evaporation rates, estimates of $K(x)$ can be obtained for all x . Details of the method, together with cross-sectional area, breadth, and surface area data for upper Spencer Gulf are given in Holloway (1974). The results of his calculations indicate that the diffusion coefficients increase from small values ($\sim 5 \text{ m}^2/\text{s}$) at Pt Augusta to an approximately constant value ($\sim 80 \text{ m}^2/\text{s}$) south of Lowly Point. In this study, the deduced variation of K has been approximated by the function,

$$K = 0.01(b_0)^{1/3} \quad b \leq 3.3 \text{ km} \\ 80 \text{ m}^2/\text{s} \quad b \geq 3.3 \text{ km}$$

The Annual Salinity Cycle

The purpose of this section is to estimate the net evaporation rates applying over upper Spencer Gulf such that the observed mean salinity distribution and annual salinity cycle are predicted theoretically using the diffusion coefficients. It is well known that pan evaporation rates obtained from shore stations are greater than the evaporation rates from neighbouring water bodies. For example, in a recent study of the water balance of flooded L. Eyre (Teitzlaff & Bye 1976), it was found that the evaporation rate over the lake was approximately 0.67 of the mean evaporation rates for Woomera, Oodnadatta and Moomba and that the proportionality factor was almost independent of the time of year. No similar comparisons between the evaporation rate for Spencer Gulf and that of neighbouring stations are known, and hence theoretical predictions of the salinity cycle have been made using a linear interpolation between pan evaporation rates (each adjusted by identical factors) at Pt Augusta and Roseworthy (Hounam 1961), and rainfall rates (Anon 1975) at Pt Augusta multiplied by a factor of 1.33 to allow for run-off, and at Wallaroo; as end points for the section (Table 1). The

TABLE 1 Evaporation and rainfall rates for Pt Augusta and Wallaroo

	PT AUGUSTA		WALLAROO	
	Evapora- tion ¹	Rainfall (mm/Month)	Evapora- tion ²	Rainfall
January	371	15	260	15
February	309	18	214	18
March	279	16	180	19
April	173	14	112	32
May	109	23	69	46
June	71	26	48	48
July	74	20	43	42
August	104	26	58	40
September	169	21	86	34
October	231	22	117	31
November	289	18	178	21
December	338	17	224	16
ANNUAL	2507	236	1589	362

¹ Pt Augusta pan evaporation

² Roseworthy pan evaporation

net evaporation rates were obtained by subtraction, and reasonable agreement with the annual mean salinity profile, and the amplitude of the annual salinity cycles along the gulf was obtained using a proportionality factor for the evaporation of 0.48

The annual mean salinity profile obtained from these data, and the annual cycle of salinity at Pt Augusta and Lowly Point, for a salinity at Wallaroo of 38‰, are shown in figures 2 and 3. They are representative of salinity data taken at various times and locations and reported in Thomas & Edmonds (1956), Holloway (1974) and Anon (1980).

It is interesting that the volume transports (due to the evaporation in the north) which maintain the salinity distributions are extremely small, for example the northward annual mean volume transport at Lowly Point

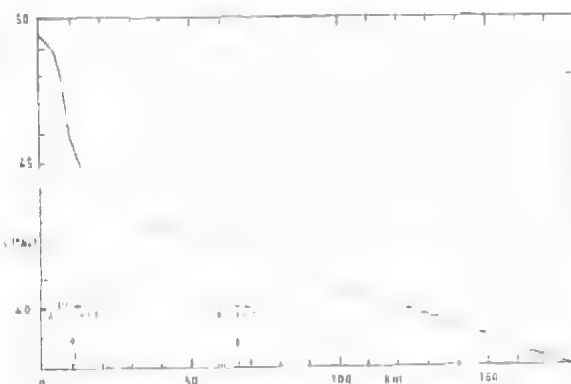


Fig. 2. Predicted profile of annual mean salinity.

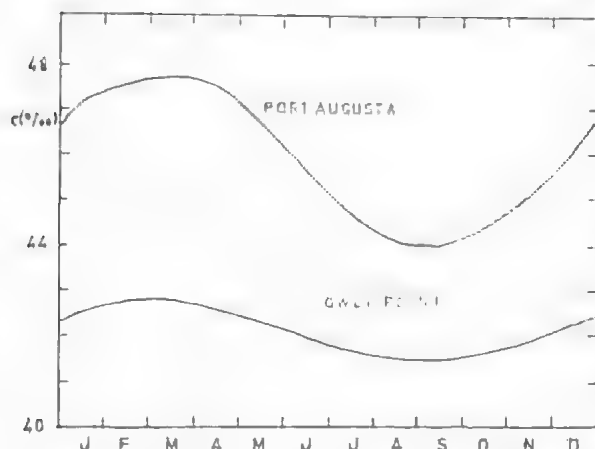


Fig. 3. Predicted seasonal variation of salinity at Port Augusta and Lowly Point.

is $8 \text{ m}^3/\text{s}$ which corresponds to a mean current of $0.05 \text{ mm}/\text{s}$. Furthermore, on dividing the volume transport into the volume of upper Spencer Gulf, we find that a period of approximately 15 years is required to renew the water volume completely. This time however has little relevance to the adjustment of the concentration profiles, since this adjustment is controlled by advection and diffusion. It would only be the time scale¹ for exchange of substance instantaneously at a uniform concentration within the gulf. The actual time scales for exchange of substances would be quite short while high transient nonequilibrium concentration profiles persist, and then lengthen steadily as the diffusive and advective fluxes tend to their equilibrium values.

These factors are reflected in a salinity variation which responds to the seasonal variations in net evaporation only partially, with a response factor, $R \sim 0.18$, where R is the ratio of the amplitude of the observed salinity cycle to that of a hypothetical cycle in complete adjustment with the annual net evaporation cycle. The corresponding lag (L) of the observed salinity cycle relative to the annual net evaporation cycle varies between 60 days at Pt Augusta and 80 days at Lowly Point.

On approximating these results by a simple harmonic cycle, in which the response factor

(R), and the lag (L) are related to the frequency (σ) of the cycle by the expressions, $L = \frac{1}{\sigma} \tan^{-1} \sigma \tau$, and $R = 1/\sqrt{1 + (\sigma \tau)^2}$ one finds that the time scale for salt exchange, $\tau \sim 300$ days.

The above results indicate that longer period climatic variability in net evaporation also may be significant in controlling the observed salinity variation. For example, a net evaporation cycle of period 5 years would have the parameters, $R \sim 0.7$ and $L \sim 200$ days, and consequently would be attenuated much less than the annual cycle.

Dispersion from within upper Spencer Gulf

Theoretical predictions for the dispersion of substances introduced within upper Spencer Gulf can be readily made for the two instances of a continuous constant production rate and an instantaneous injection of a fixed quantity of substance. For definiteness the substance will be introduced at a location 34 km from the head of Spencer Gulf (Fig. 1), and 24 km south of Pt Augusta.

(1) A continuous production rate of $6 \text{ kg}/\text{s}$ for a conservative tracer

The concentration pattern for a conservative tracer ($d = s = 0$) is shown in Figure 4. The concentration falls sharply south of the source, and is approximately constant north of the source with a value of 48 ppm ; the Lowly Point concentration being 15 ppm . The small rise north of 34 km mirrors the salinity distribution since the fields are both source free in this region. The total mass of substance in the steady-state equilibrium above Lowly Point

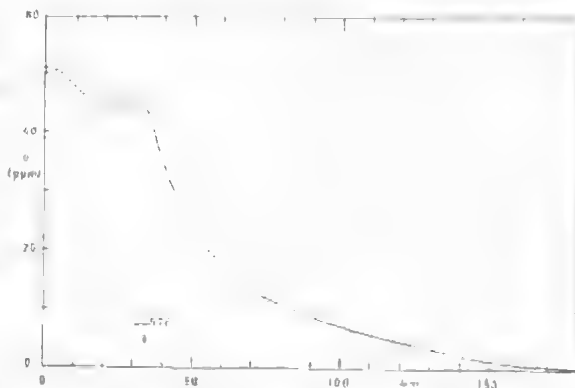


Fig. 4. Predicted concentration profile for conservative tracer for continuous source of $6 \text{ kg}/\text{s}$ located 34 km from head of Spencer Gulf.

¹ The time scale (τ) is defined as the non-equilibrium mass of substance in upper Spencer Gulf divided by the southward flux of substance past Lowly Point. Time scale is used rather than time constant since τ may vary appreciably with t . The mass and flux are positive quantities for loss, and negative quantities for gain of substance.

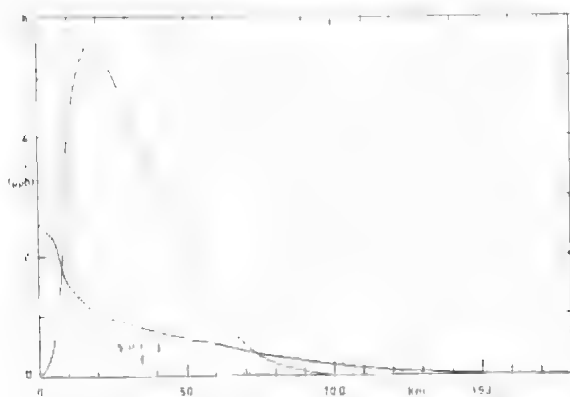


Fig. 5. Predicted concentration profiles 40 and 200 days after instantaneous release of 10 t of conservative tracer at location 34 km from head of Spencer Gulf.

is 90 kt, and hence its residence time in upper Spencer Gulf is 180 days. This residence time is less than the exchange time scale for salt of 300 days, due to the concentration gradients being relatively greater than for the distribution of an introduced substance than for salt, and leading to a more rapid dispersion. In fact the residence time is controlled almost exclusively by lateral diffusion (cf. Table 3).

(2) *An instantaneous source of 10 t of a conservative tracer*

The distribution pattern initially shows a lateral dispersion approximately symmetrically centred on the source. After about 150 days however the northward dispersion impinging on the head of the gulf has redistributed the substance in a similar manner to the steady-state concentration pattern (Fig. 5). Thus at Pt Augusta a maximum in concentration of 5 ppb occurs after about 60 days.

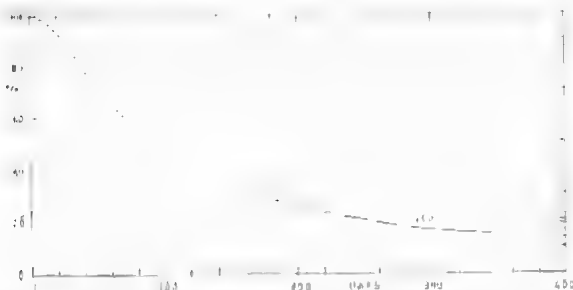


Fig. 6. Predicted percentage of instantaneous release located 34 km from head of Spencer Gulf, north of Lowly Point, as function of time after release. (---) indicates loss time scale in days.

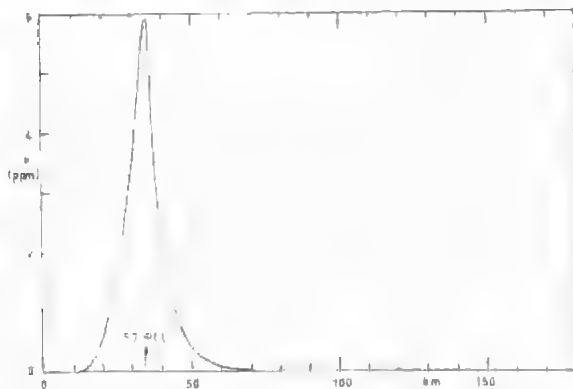


Fig. 7. Predicted concentration profile for tracer which exchanges with atmosphere for continuous source of 6 kg/s located 34 km from head of Spencer Gulf.

The dispersion past Lowly Point is characterised by an initial interval of small loss prior to the arrival of substance by diffusion, followed by a loss which decreases in rapidity as the concentration decreases (Fig. 6). In fact, initially the loss time scale is about 120 days, but this increases to about 250 days when only 25% of the substance remains.

For the reasons discussed previously, the characterisation of the loss process by a simple exponential law is clearly not adequate. An approximate analysis indicates that the loss time scale (τ) in fact increases exponentially with time, i.e.

$$\tau = \tau_0 e^{t/\tau'}$$

in which τ_0 and τ' are constants, that for the location of the instantaneous source have the approximate values, $\tau_0 = 110$ days, and $\tau' = 350$ days. Thus although the initial stage of the dispersion is relatively rapid, the final stage is highly protracted.

(3) *A continuous production rate of 6 kg/s with surface exchange*

The distribution of a substance with a decay time constant of less than ~ 100 days would be expected to be changed significantly from that for the conservative substance. In particular, for exchange with the atmosphere a typical exchange velocity, $\mu = 10^{-5}$ m/s (Haney 1972), thus at 34 km the local decay time constant ($\frac{A}{\mu h}$) would be about 6 days. This

short decay time constant causes a large reduction in concentration in comparison with the conservative tracer (Fig. 4); the maximum value of 6 ppm now occurring at the source (Fig. 7).

The above result can also be interpreted in terms of the temperature field arising from a heat source with subsequent atmospheric exchange. For example, for a discharge (q) of 10^6 m³/day at an excess temperature (ΔT) of 5°C, the apparent source,

$$\int_{x_s}^{x_s'} p dx = \rho q \Delta T$$

where x_s and x_s' are the bounds of the source, and the concentrations in Figure 7 correspond approximately to excess water temperatures in 1/100th of °C, e.g. the maximum excess on the scale of averaging of the calculation (2 km) is 0.06°C, and is aligned with the source. In the near field however much higher temperature anomalies would occur, and the diffusive heat flux divergence would be negligible compared with the surface exchange flux, so that for a semi-circular temperature distribution appropriate to a source on the coast, one obtains,

$$T(r) = \Delta T e^{-(r/r_0)^2} \quad r \ll h(x)$$

where r is the radial co-ordinate, and $r_0 = (2q/\pi\alpha)^{1/2}$ is the decay length. The travel time to r_0 , $t_0 = h/\mu$, where h is the thickness of the surface heated layer, and thus approximately the near field temperature structure has a length scale, $r_0 = 1$ km, and on assuming that $h = 0.1$ m, a time scale $t_0 = 3$ hrs.

(4) *The effect of long period changes in water level*

It is known that long period changes in sea level distinct from the astronomical tides occur along the south coast of Australia (Provis & Radok 1979). These fluctuations in sea level, which typically have a magnitude of 0.2 m, propagate into Spencer Gulf, and those of long period (≥ 1 week) cause the sea levels in upper Spencer Gulf to change approximately uniformly.

The effect of the level changes is to oscillate the water longitudinally with a range of $2a \pm/\Lambda$, where a is the vertical amplitude of the long period motion. The ratio \pm/Λ is almost constant with distance, varying from about 2500 at Pt Augusta to 4000 at Wallaroo. Thus for $a = 0.2$ m, the range of the water particles is 1–2 km, and this leads to cyclic changes of salinity of amplitude 0.03‰ at Lowly Point and 0.4‰ at Pt Augusta. Otherwise no important effects on the property distributions are expected.

Conclusions

Several matters which follow from the discussion of the previous sections, can now be considered.

(1) *The accuracy of the estimates*

The main question concerning the estimates is of course their accuracy. The principle of the analysis has been to reproduce reasonably well the mean salinity profile, and the annual salinity cycle, and then to predict the dispersion of other substances. No data sets are known to exist for the distribution of other substances however which can provide independent checks on the deduced mixing parameters.

In view of this situation recourse must be made to a theoretical error analysis. Table 2 shows the variation in mean annual salinity levels at Pt Augusta and Lowly Point that would occur for diffusion coefficients and net evaporation rates varying from those of the analysis by factors of 1.50 and 0.75. The most important conclusion is that the mean salinity levels are determined by the ratio $(E-R)/K$, (cf. Determination of the diffusion coefficients). Thus the vigour of the exchange process is *not* monitored by the mean salinity profile. The vigour however is monitored by the observed salinity cycle, such that for a

TABLE 2. Predicted mean annual salinities and the seasonal salinity range for various $(E-R)$ and K

(A) MEAN ANNUAL SALINITY (‰) ¹					
		(E-R)			
FACTOR ²		0.75	1.00	1.50	
K	0.75	45.8	48.7	55.1	
		42.0	43.4	46.4	
	1.00	43.7	45.8	50.2	
		41.0	42.0	44.2	
	1.50	41.7	43.0	45.8	
		40.0	40.6	42.0	
(B) SEASONAL SALINITY RANGE (‰) ³					
FACTOR ²					
(E-R)	K	PT AUGUSTA		LOWLY POINT	
1.50	1.50	48.4	43.4	43.0	41.1
1.00	1.00	47.8	44.1	42.7	41.4
0.75	0.75	47.6	44.4	42.6	41.4

¹ The two values are respectively the mean annual salinity at Pt Augusta and Lowly Point.

² The factor 1.00 corresponds to that for the main calculations, the other factors are multipliers for $(E-R)$ or K .

³ The two values are respectively the maximum and minimum salinities during the annual cycles.

TABLE 3. Predicted residence time in days for a continuous conservative source located 34 km from the head of Spencer Gulf for various (E-R) and K

FACTOR ¹	0.75	(E-R) 1.00	1.50
0.75	237	240	245
K 1.00	176	178	180
1.50	116	117	119

¹ The factor 1.00 corresponds to that for the main calculations, the other factors are multipliers for (E-R) or K

constant (E-R)/K the amplitude of the salinity cycle is reduced as E-R (or K) is increased. This trend nevertheless is not well marked (Table 2), and hence the true solution for E-R and K cannot be defined precisely from the available data. In the event that the proportionality factor for the pan evaporation is too small, a reduction in the time scales for dispersion would occur, e.g. for a pan factor of 0.67 (cf. L. Eyre) the residence time for a continuous conservative source would be reduced from 180 days to 130 days (Table 3). Similar reductions would apply for other time scales, and the diffusion coefficients south of Lowly Point would have the value 110 m²/s instead of 80 m²/s. Thus it is probable that the dispersion estimates have an accuracy of about 25%, with the likely bias (from considerations of the net evaporation) being towards time scales somewhat less than those found using Holloway's estimates of the diffusion coefficients.

(2) Additional factors

Wind effects have not been considered explicitly since it is probable that the main agent of the turbulence is the tidal current; however a proportion of the mixing may be wind induced, and thus one would expect some seasonal variation in the diffusion coefficients. It is not anticipated however that individual storms would have a large effect on the dispersion processes. Periods of calm associated with minima in the tidal current amplitudes such as occur around 'dodge tides' also may have a transient effect on mixing by allowing a stratified flow regime to exist.

All these effects have their place, however an average corresponding to the salinity dis-

tribution is perhaps that which is required initially in a study of tracer distributions, and data suggest that the salinity distribution is a reasonably well defined regime within the recent 25 years during which measurements are available (Thomas & Edmonds 1965; Holloway 1974; Anon 1980).

The special behaviour of tracers other than well vertically mixed conservative and atmospherically exchanged quantities also has not been considered, for example, the behaviour of surface and bottom seeking substances would be significantly different and require individual treatment. A comprehensive treatment of course must extend to an evaluation of the results of exchange of substance for marine life and for the atmosphere.

(3) Proposed programmes of observation

A fuller understanding of the dispersion process would of course rely on extended programmes of observation. In particular, observations of the actual water balance of upper Spencer Gulf, including evaporation, rainfall and run-off are required as time series extending over several years. These data could then be used together with observed profiles of salinity, and other introduced tracers to specify in detail the dispersion process. In particular, attention should be given to the conditions just south of Lowly Point which control the response of upper Spencer Gulf to the north.

In summary, the property distributions in upper Spencer Gulf are derived from an interesting balance between the net evaporation and lateral diffusion, and are a good example of what has been called a 'reverse estuary'. Several similar inlets exist around the Australian coastline (notably in Western Australia) for which this kind of analysis would also appear to be applicable

Acknowledgements

The ideas presented in this paper have been stimulated by the necessity for obtaining some understanding of the dispersion regime in upper Spencer Gulf in the event of the proposed industrial development at Redelf, which is situated 34 km from the head of Spencer Gulf, approximately at the source location used in the dispersion studies.

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BY R. J. F. JENKINS, P. S. PLUMMER & K. C. MORIARTY

Summary

Enigmatic, subcylindrical to conical, sediment-infilled structures occurring in the Trezona Formation and the lower and upper parts of the Moorillah Formation of the late Precambrian of the central Flinders Ranges, South Australia, resemble certain fossil burrows such as *Bergaueria* Prantl, and also late Precambrian body fossil remains including the sack-shaped, soft-bodied form *Ernietta* Pflug from South West Africa (Namibia). The structures occur up to 3,300 m stratigraphically below the well known Ediacara assemblage. The lack of disruption or vents in their matrix seemingly negate the possibility that they are water escape structures, but studies of their infilling and literature research indicate that their true origin is almost certainly inorganic, their resemblance of various fossil remains being fortuitous. Their recognition emphasizes the apparent non-occurrence of metazoan remains below the Ediacara assemblage in the local rock record, lending negative support to recent theories postulating either late evolution of the Metazoa or rapid diversification of animal life in the latest Precambrian.

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Enigmatic, subcylindrical to conical, sediment-infilled structures occurring in the Trezona Formation and the lower and upper parts of the Moorillab Formation of the late Precambrian of the central Flinders Ranges, South Australia, resemble certain fossil burrows such as *Bergaueria* Prantl, and also late Precambrian body fossil remains including the sack-shaped, soft-bodied form *Ernieita* Pflug from South West Africa (Namibia). The structures occur up to 3,300 m stratigraphically below the well known Ediacara assemblage. The lack of disruption or vents in their matrix seemingly negate the possibility that they are water escape structures, but studies of their infilling and literature research indicate that their true origin is almost certainly inorganic, their resemblance of various fossil remains being fortuitous. Their recognition emphasizes the apparent non-occurrence of metazoan remains below the Ediacara assemblage in the local rock record, lending negative support to recent theories postulating either late evolution of the Metazoa or rapid diversification of animal life in the latest Precambrian.

Introduction

In 1975, a discovery of abundant, peculiar cylindrical structures was made by Moriarty in the lower part of the Moorillab Formation (Plummer 1978) in Utanouna Creek, within the Bunbinyunna Range, south-west of Wilpena Pound in the Flinders Ranges (Fig. 1). At the time he considered that the structures may have been biogenic. During late 1976, in the course of extensive field mapping of the Brachina Subgroup, Plummer found a comparable structure in float within Bunyerroo Creek, and later a second specimen only a few kilometres from the original find of Moriarty. This latter specimen was shown to Jenkins who noticed a radial pattern of markings on the base of the (short) column, and longitudinal striations on its sides. As such, the form showed a resemblance to the Cambrian to Jurassic trace fossil *Bergaueria* Prantl, and also to various late Precambrian metazoan remains. Subsequent exploration has widened the known distribution of the structure and confirmed its constancy of general form and the more or less stable sedimentological characteristics attending its preservation.

Two specimens of similar structures in stratigraphic collections of the University of

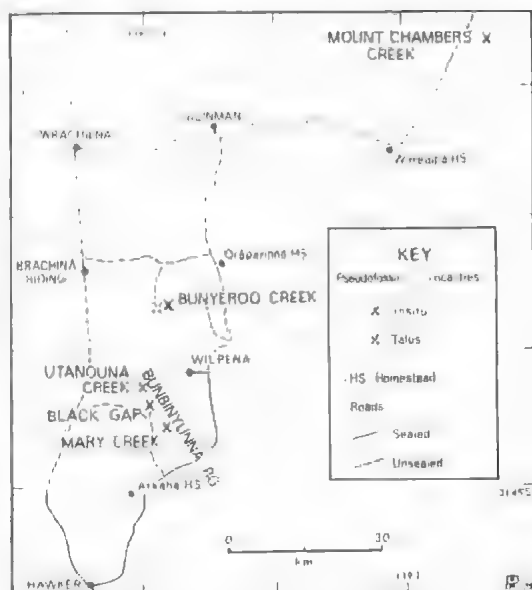


Fig. 1. Locality map of pseudofossil occurrences in central Flinders Ranges, South Australia.

Adelaide were found by M. A. Reynolds in 1950 west of "Bunyerroo Hut" (probably Yannyanna Hut on current maps) apparently within the Trezona Formation of the Umberatana Group.

Stratigraphy

The Trezona Formation reaches a thickness of about 240 m in the Orparinna area and consists of mud flake rich pelletal limestones,

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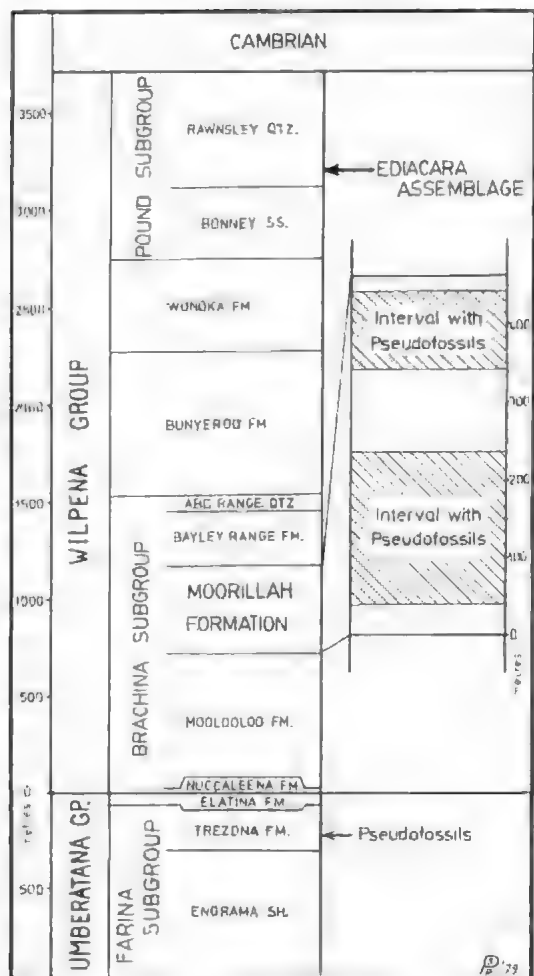


Fig. 2. Chart summarizing regional stratigraphy of youngest Precambrian succession in central Flinders Ranges, and showing stratigraphic intervals in which pseudofossils are found in relation to Ediacara assemblage. Only upper part of Umberatana Group shown. Pound Subgroup after Jenkins (1975b).

cryptalgal-laminites and associated stromatolites, oolitic limestones and intraformational limestone conglomerates interbedded in green siltstones (Thomson *et al.* 1976). It is of shallow water origin and comprises the uppermost unit of the Farina Subgroup, within the Umberatana Group, and is of early Marinoan age in terms of the local late Precambrian time-rock stratigraphy (Thomson 1969). It is succeeded by the approximately 60 m thick Elatina Formation which includes the tillitic deposits of the third and youngest glacial phase of the Adelaidean (Mawson 1949), and is part of the Willochra Subgroup of the Umberatana Group.

The Brachina Subgroup (Plummer 1978) of the Wilpena Group is a coarsening upward, dominantly clastic sequence with an average thickness of 1500 m. It rests mostly conformably though locally disconformably on the Elatina Formation. Lying within the Subgroup approximately 600 m above this glaciogenic unit is a 460 m thick sequence consisting predominantly of thinly interbedded red and purple shales and siltstones. This sequence is defined as the Moorillah Formation and commonly interposed within it are medium to thick beds of purple tuffaceous siltstone which often display intraformational conglomeratic textures, and lenticular crossbedded sandstones. Soft-sediment deformation structures are ubiquitous.

The structures which form the subject of this paper occur in two broad intervals within the Moorillah Formation. In Bunbinyunna Range (Fig. 1) several hundreds of specimens were observed in a broad zone spanning much of the basal half of the Formation. Very few specimens were observed near the top of the Formation in this area. Specimens were, however, moderately numerous near the top of the Formation at Mount Chambers Creek, 100 km to the northeast.

Repositories

Representative specimens are lodged in the collections of the University of Adelaide: catalogue numbers prefixed "A.U.". Studies were also made of a large collection of late Precambrian fossils obtained by Dr Hans Pflug, Giessen, West Germany, from the Nama Group of Namibia (South West Africa). These specimens, catalogued "Pf." are ultimately to be returned by Dr Pflug to the appropriate statutory body in Windhoek.

Description

The shape of the structures in vertical section is commonly cylindrical (Fig. 3A & E), with either a rounded to hemispherical base (Fig. 4A), or a flat, U-shaped base (Fig. 3F; Fig. 4G), which is often lopsided and with one or several central indentations (Fig. 4C, D, E & F). A sub-conical shape is also occasionally displayed (Fig. 3B & C). The upper part frequently expands outwards like the mouth of a trumpet. In section parallel to the bedding the structures display a circular to ovoid outline (Fig. 3C & D). The width of the structures (disregarding the trumpet-like upper rim) averages 6–8 cm, but

varies between 0.8 and 20 cm. The expanded mouth of the trumpet may reach over 30 cm. Their width is frequently less than their depth, with some specimens roughly twice as deep as wide. The depth may reach about 20 cm. Often their surface is nearly smooth, but on many a series of fine longitudinal ridges and grooves extends along the cylinder or cone and fans out on the trumpet-like upper rim. Occasionally these ridges and grooves continue across the base of the structure as radial markings (Fig. 4F). The significance of these markings is questionable, however, as they are often indistinguishable from, and grade into slickensides which also occur commonly within the matrix.

In the Moorillah Formation the structures are found within interbedded shales, siltstones and fine sandstones. In the majority of specimens the base of the structure is either sunken down into, or in close juxtaposition with the top of a siltstone or fine sandstone bed (Fig. 4C). The upper parts of the structures are often enveloped by laminated shales which sometimes include thin beds of siltstone. Where the siltstone below the structures is thin it is sometimes bowed downwards and there is a tendency for the shale laminae and thin siltstones subjacent to the sides of the structures also to be gently curved downwards (Fig. 3A & E; Fig. 4C & D). The uppermost part of the structures may terminate within shale, or be truncated or capped by another bed of siltstone which is often bowed upwards. The capping shale or siltstone participated in partially filling the structures. Rare specimens occur more or less entirely within shale (Fig. 3F).

Sections of the structures show that they had a complex history of infilling and subsequent compaction (Fig. 4C, D, E & G). Often the initial infilling consists of fine to coarse sand with angular or subrounded mud and silt clasts which came to rest in a sub-horizontal attitude, or sometimes in an edge-wise fashion (Fig. 4G). The sand infilling may show rather irregular erosional surfaces within, or grade upwards into laminated siltstone still containing occasional clasts. It is apparent that during de-watering of the surrounding matrix appreciable compaction occurred. The sandy material and silty infill of the forms seems generally to have behaved in a more competent manner and compacted less than the enveloping matrix, resulting in the observed

downward deformation of the external sediments below and upward deformation above (Fig. 3E). The silt laminae of much of the infill are frequently bowed upwards (Fig. 4C, D & E). The specimens from the Trezona Formation have a slightly calcareous silty infill, but otherwise show similar characteristics to the material from the Moorillah Formation.

Interpretation

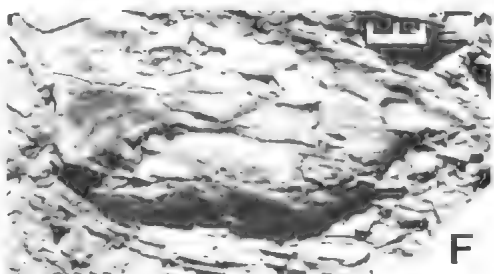
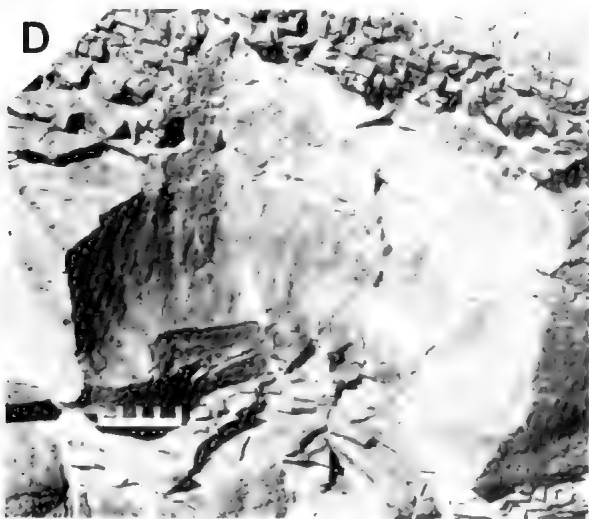
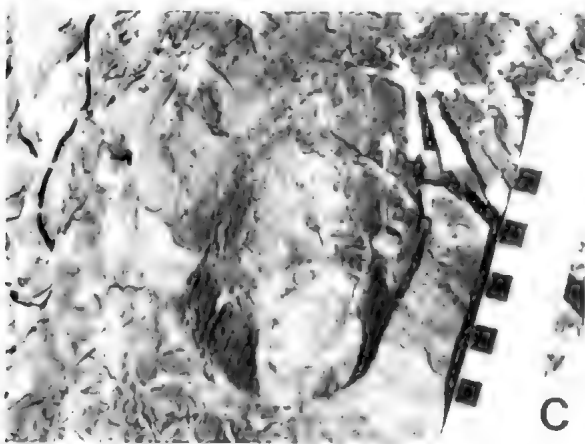
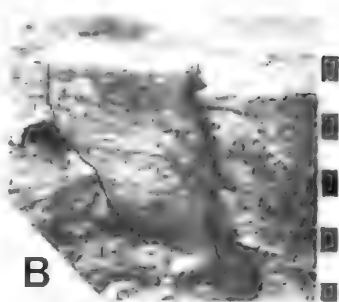
General

The nature of the infill indicates that the structures must have initially been hollows or holes within the sedimentation surface. These holes thus acted as traps for any coarse sediment being carried in traction before being buried by the more turbid finer sediment. A syngenetic origin is therefore envisaged for which either an organic origin, or production by inorganic processes, is possible.

Possible Organic Origin

Two possible organic origins could produce syngenetic structures similar to those described here. Firstly, the burial of dwelling or hiding burrows of actinian-like creatures could produce trace fossils resembling such forms as *Bergaueria*, or *Conastichus* Lesquereux. Alternatively, the preservation of eup- or sack-shaped animals could yield body fossils comparable to *Namulia* Germs, the "Ernettomorpha" of Pflug (1972a) or *Baikalina* Sokolov.

Frey (1970) describes the burrows of several living actinians as being considerably deeper than wide, or sometimes extremely elongate and occasionally branched. Shinn (1968) shows that adjacent to such burrows it is common to see a downwarping of the sediment lamination. In a study which Mangum (1970) made on the burrowing behaviour of the anemone *Phyllactis* Milne Edwards & Haine, she stated that rhythmic contractions of the column musculature manipulate the fluids of the column's hydrostatic skeleton to push the pedal disc into the substrate; "after the pedal disc reaches a hard substratum and sand surrounds the column (burrowing) ceases." The Lower Cambrian to Jurassic trace fossil *Bergaueria* is normally attributed to actinians burrowing and resting in this manner (Crimes *et al.* 1977). According to Alpert (1973) the depth of *Bergaueria* is less than or equal to its diameter, although Crimes *et al.* have observed deeper specimens in the Lower Cambrian of Spain. Externally,



some of our more shallow specimens are essentially indistinguishable from *Bergaueria* except for being generally greater in size. Sectioned specimens of *Bergaueria* from the early Cambrian of Alberta, Canada (Needler Arai & McGugan 1968; Germs 1972a) show a coarser, less regular internal lamination than our material, and sometimes show slumping which is presumed to reflect decomposition of the inhabitant of the burrow.

More conical examples among the present structures show a marked resemblance to another trace fossil, *Conostichus*, which is best known from the Mississippian-Pennsylvanian of North America and is also attributed to burrowing actinians (Chamberlain 1971; Crimes *et al.* 1977). *Conostichus* is a more or less conical burrow, tapering downwards, reaching about 11 cm in depth and 8 cm in diameter (Branson 1960) and variably marked by transverse constrictions and longitudinal furrows and ridges. The sides of *Conostichus* consist frequently of several "packed" layers apparently formed as the anemone wallowed in its burrow. Where it is assumed that the actinian abandoned the burrow abruptly, "shifting sand and debris filled the void with cross laminae" (Chamberlain 1971). Where the actinian apparently migrated upward in order to keep pace with sedimentation, the centre of the burrow may be filled with transverse sand laminae forming apically-convex concentric cones. While the present structures are sufficiently similar to *Conostichus* to suggest that they could have a broadly similar biological origin, that is formed by a "poly-poid" organism largely buried in the substrate, some important differences are apparent. Our structures are never observed to show layers of sediment plastered subjacent to their walls, and both the even lamination or the small erosional features within the infill show that the origin of this material is entirely sedimentary and not the packing behind a polyp moving upwards in its burrow.

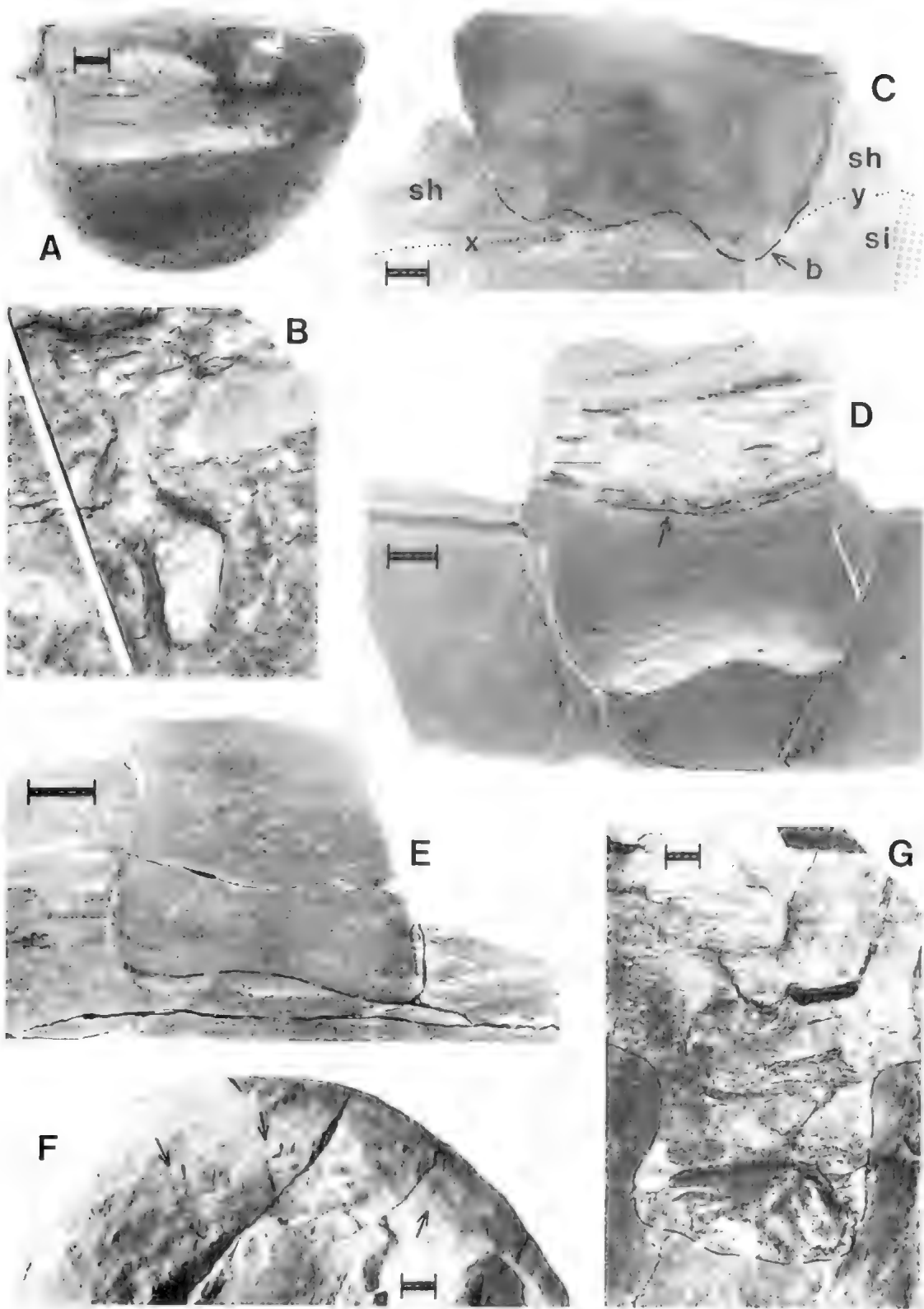
The second possible organic interpretation of the structures is that they are actual body

fossil remains, with the integument of the organism represented by the surface of parting between the enclosing matrix and the infilling material. They could thus be considered to be preserved as either an external mould and counterpart cast or as composite moulds in the terminology of McAlester (1962) and Wade (1968, 1971). As such, they might be further interpreted as showing affinities with a rather variable group of fossil forms known from the late Precambrian. These forms are *Namalia villiersiensis* Germs and the variety of specimens which Pflug (1972a) includes in the "Erniettomorpha", both from the Kuibis Subgroup of the lower part of the Nama Group, Namibia, and *Baikalina sessilis* Sokolov from the Ayankan Formation of the Upper Yudomian, on the Malyi Anai River, near Lake Baikal in Siberia.

Our structures strikingly resemble *Namalia villiersiensis* and the variable fossils Pflug (1972a) collectively describes as the "Erniettomorpha". Within this division Pflug includes 13 genera with 28 species in five subfamilies, four families and two orders (Glaessner 1979). One of us (Jenkins) has examined Pflug's material and considers that all the specimens he refers to as the "Erniettomorpha" belong to a single genus and species, *Ernietta plateauensis* Pflug; the other nominate taxa seemingly differ only in their completeness of preservation, their degree of compression, or the amount by which syndepositional erosional processes have truncated the upper parts of the buried remains (see also Glaessner & Walter 1975). The remains of *E. plateauensis* seem so similar to *N. villiersiensis* in their morphology, preservation and provenance that it is very likely that they are conspecific.

Ernietta is usually preserved in apparent life position with recorded field occurrences (Germs 1968, 1972a, 1972b) and specimens (Pflug collection) indicating that numerous individuals lived in close proximity to one another. The organism was essentially sack-shaped in form (Fig. 5A, B, C & E; Fig. 6A)

Fig. 3. Field photographs of uncollected pseudofossils; examples from lower part of Moorillah Formation, except D and F from upper part; scale divisions in cm. A, subcylindrical form with beds in adjacent matrix curved downwards at sides and thinned near base: Utanouna Creek. B, conical specimen: Utanouna Creek. C opening where conical specimen has eroded from matrix; upper edge of form apparently extended to line x-y and striations on mould of its surface are arrowed: Black Gap. D, external mould of large bowl-shaped form: Mount Chambers Creek. E, subcylindrical specimen showing gently domed ripple bedded sands above and downward deformation of beds near base: Utanouna Creek. F, profile of shallow structure within shale: Mount Chambers Creek.



and composed of several layers of soft tissue which could undergo ready deformation. The sack is inferred to have been attached at its closed end, either to the substrate, or very frequently to small clay gulls or some other projection on the surface of the substrate (Fig. 5D & E; Fig. 6A). The several wall membranes of the sack were interconnected by thin, flexible, radially arranged, longitudinal septa whose position on any particular wall layer is marked by either narrow ridges or fine longitudinal grooves (Fig. 6B, C & D). The elongate tubular spaces so formed between the walls and the septa are frequently packed with silt or sand to form internal moulds. The upper and apparently open end of *Ernietta* terminates in a crenellate margin in the few rare instances where it is preserved. More frequently, however, it is found collapsed and deformed (Fig. 5A & E). This discussion of other details concerning the structure of this extraordinary organism fall outside the scope of the present work.

One of the most remarkable characteristics of *Ernietta* is its preservation, which is one of infilling comparable to the structures from the Flinders Ranges. Thus, sections of *Ernietta* may show a layered and graded sand or silt infill, with medium-grained sand at the closed end of the sack and very fine-grained sand near the apparent open end (Fig. 5C). Bedding surfaces indicate the original depositional orientation. Blebs of clay-rich material and limonite pseudomorphs, presumably after authigenic pyrite, are frequent in the infillings. The few specimens still within their original matrix are enveloped by medium-grained sand (now quartzite). The infilling of *Ernietta* does not, however, show the fine lamination usually observed in our structures.

Pflug (1972b 1974) orientated the "Ernietomorpha" in the reverse aspect to that sug-

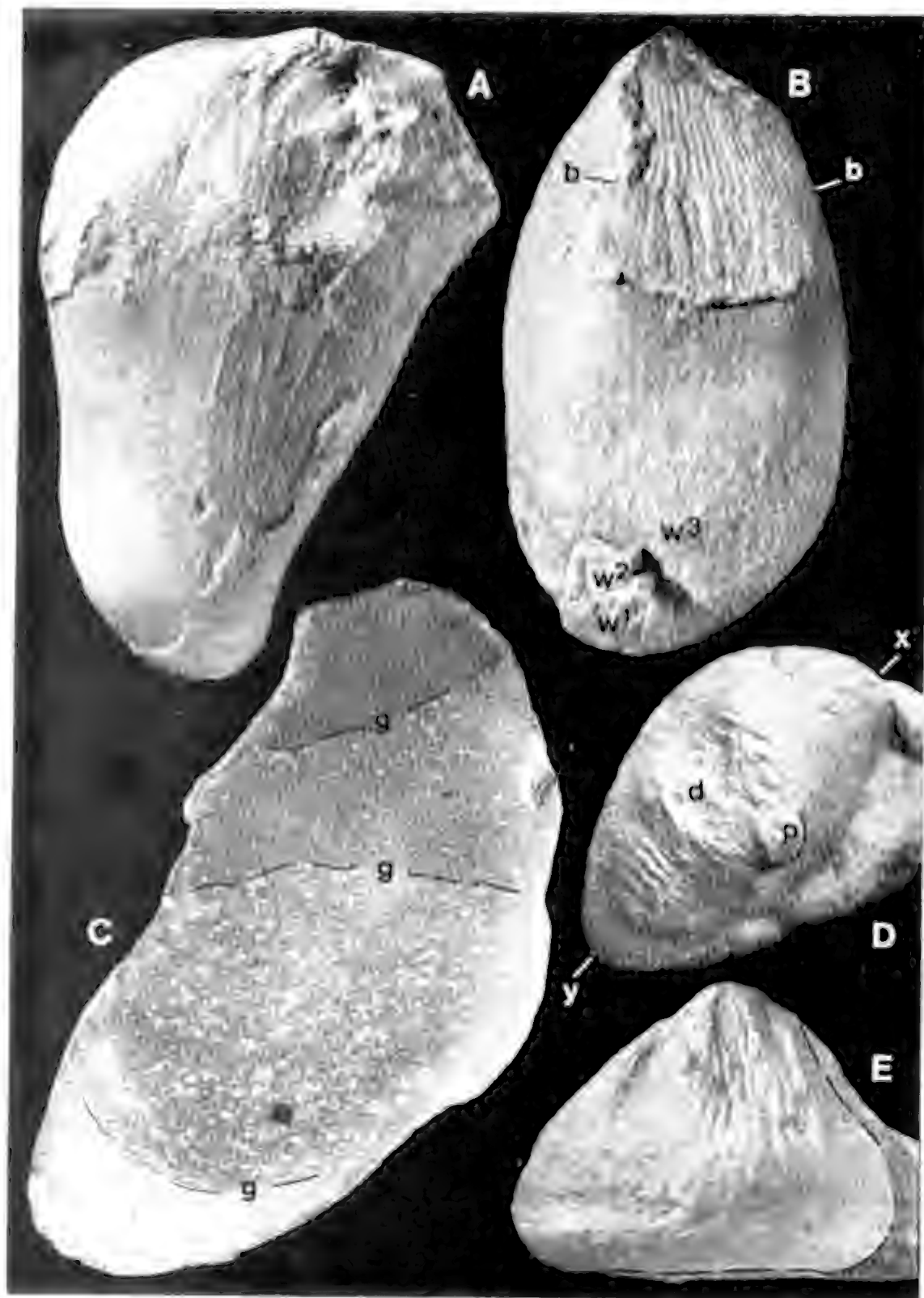
gested here, that is with the closed end of the sack upwards. Published data concerning their occurrence in the field (e.g. Germs 1968, 1972a) are ambiguous as to their orientation. Nevertheless, evidence from their distortion and layered infill is considered substantive of our interpretation.

From a stratigraphic viewpoint it is intriguing that the Kuibis Subgroup, which contains *Ernietta*, is succeeded by a sequence containing glaciogenic sediments and scraped and grooved bedding planes (parts of the Schwarzrand Subgroup) reflecting several cold phases of later late Precambrian glaciation in southern Africa (Germs 1972a, 1974; Kröner 1977; Kröner *et al.* 1980) and that our structures occur only relatively short stratigraphic distances both below and above the last late Precambrian glaciogenic deposits in the Flinders Ranges (parts of the Elatina Formation). However, the glacial events recorded in the Schwarzrand Subgroup are suggested to have been of local extent, and radiometric data of relevance for the Nama Group (Kröner 1977; preliminary data passed in personal communication between Professor Kröner and Dr Pflug; Kröner *et al.* 1980) together with fragmentary dating information from Australia reviewed by Williams (1975) suggests the likelihood that the Nama glaciations are significantly younger than the Elatina Formation.

The Siberian form *Balkania sessilis* is apparently closely similar to *Ernietta*, but is too incompletely described for further comparison.

One objection to a biological origin is that if our forms did represent soft-bodied fossil organisms then the creatures must be interpreted as having maintained their life functions even during the time of their infilling, as their presumably soft integument would surely have collapsed flat if death were earlier.

Fig. 4. Photographs of infilling sediment and sections of pseudofossils and field photograph of depressions connected by gullers from lower part of Mnorillah Formation at Utanouna Creek, except F, from same stratigraphic interval at Black Gap and G from loose boulder in Bunyeroo Creek. Bar-scales equivalent to 1 cm. A, side view of plug of infilling sediment of pseudofossil eroded free, A.U. No. 24731. B, field photograph of irregular depressions interconnected by gullers; end of ruler to hinge 50 cm. C-E, reflected light photographs of sections of pseudofossils; C, erosive base (b) of form closely juxtaposed with bedding interface (x-y) between siltstone bed (st) and overlying shale (sh), A.U. No. 24729. D, east infill with erosive surface, arrowed and cone-shaped fractures (f-f) extending below; shale laminae in matrix down-turned at sides of structure, A.U. No. 24730. E, specimen with centrally domed base and domed, finely laminated silt infilling, A.U. No. 24728. F, underneath view of part of base of infilling plug of large pseudofossil with arrows indicating more or less radially arranged markings, A.U. No. 24733. G, broken section through pseudofossil within fine sandstone; infilling, also fine sandstone, includes numerous shale flakes, some of which are orientated in edge-wise fashion; overlying bed of laminated fine sandstone, A.U. No. 24734.



Maintenance of life during sedimentation seems manifestly impossible. This argument makes the explanation of the preservation of *Ernietta* difficult, but for this form it might be presumed that the onset of sedimentation was extremely rapid, perhaps in the form of a turbidity current which gave rise to the observed graded infill. In any event, the *Ernietta* organisms appear to have ultimately succumbed to sedimentation as their tops are variably pursed and compressed or overfolded (Fig. 5A & E). Our structures show no evidence of the multiple wall tissues present in *Ernietta*, nor definite evidence of septa or the precise and regular organization so characteristic of this fossil form. The most convincing explanation of the striations on the sides of our structures are as slickensides due to differential compaction. In a number of specimens the slickensided surfaces project into the matrix below the actual infill in the form of a more or less cone-shaped fracture (Fig. 4B).

The systematic position of *Namalia*, the "Erniettomorpha" and *Baikalia*, together with several other problematic Precambrian fossil organisms, was reviewed by Glaessner & Walter (1975), who suggested them to be related to their taxon *Arumberia hanksi*, from the Arumberia Sandstone in the Amadeus Basin, central Australia. Glaessner & Walter considered that while these forms could generally be referred to Pflug's (1970a, 1970b, 1971, 1972a, 1972b) division of the "Petalonamae", the formal application of this name was not to be recommended because of its hypothetical concept and various speculative implications applied to it. Thus they rejected the ideas of Pflug (1973, 1974) that the "Petalonamae" represent a peculiar branch of Precambrian evolution intermediate in position between the kingdoms of plants and animals. Nevertheless, Glaessner & Walter maintained that the forms just discussed and various Precambrian frond-like organisms show a general

similarity which implies an underlying taxonomic unity, and that the members of this grouping "may be classified provisionally as Coelenterata of uncertain systematic position".

This viewpoint is criticised by Jenkins and Gehling (1978) who suggested that the original concept of the "Petalonamae" may involve the artificial amalgamation of quite distinctive classes or even of separate phyla. Varying further interpretations of the Petalonamae are given by Ford (1979), Brasier (1979), Scrutton (1979) and Glaessner (1979), but this problem falls essentially outside the scope of the present study. Based on comparison with the geological studies and experimental work of Dżułyński & Walton (1965), "*Arumberia*" is considered by Brasier (1979) to be "probably a pseudofossil caused by turbid water flows". New widespread discoveries of "*Arumberia*" made by Dr B. Daily and Jenkins in central Australia (see also Kirschwink 1978), where the form is several times found in near association with coarse grained sandstones or conglomerates, provide a body of additional evidence supportive of Brasier's conclusion.

Probable Inorganic Origin

In an excellent review of inorganic cylindrical structures found within sediments, Bailey & Newman (1978) indicate that the usual postulated mechanisms for their formation involve early diagenetic upward-flowing springs or escaping pore waters (see also Quirke 1930; Hawley & Hart 1934; Gabelman 1955; Conybeare & Crook 1968). Such structures are frequently filled with sediment of similar grain size, sorting and texture to the enclosing (siltstone or sandstone) matrix, or show a crude coarsening in grain size towards the centre of the cylinder. Occasionally, even an inverted cone-in-cone arrangement of silt and sand lamination can occur (see Dionne & Laverdière 1972; Gangloff 1974). Often the lower end of the cylinder is irregular and shows

Fig. 5. Remains of *Lametta photactensis* Pflug, 1966, from Kuibis Subgroup of lower part of Nama Group, Namibia; all natural size. A, side of nearly complete specimen viewed along line of wider transverse axis; uppermost parts show evidence of overfolding, Pf. No. 178. B, side of specimen viewed normal to wider transverse axis; at least three separate wall membranes (W_1 , W_2 and W_3) shown by internal moulds of sand, enigmatic "budding" suture occurs along b-b, Pf. No. 182. C, longitudinal section of sand infilling central cavity showing layers of progressively finer sediment and depositional surfaces (a) presumably reflecting intermittent stages of infilling and termination of organism at each stage; dark square and spots, limonite after authigenic pyrite, light coloured edge of the infilling due to weathering Pf. No. 308. D, view of base of specimen showing deformed area (d) and nipple-like prominence (p) which may represent the point of attachment of the organism; zig-zag suture along line x-y, Pf. No. 99. E, side view of specimen with some of enclosing matrix; infilling individual collapsed downwards, with base flattening and upper part pursing inwards, Pf. No. 287.

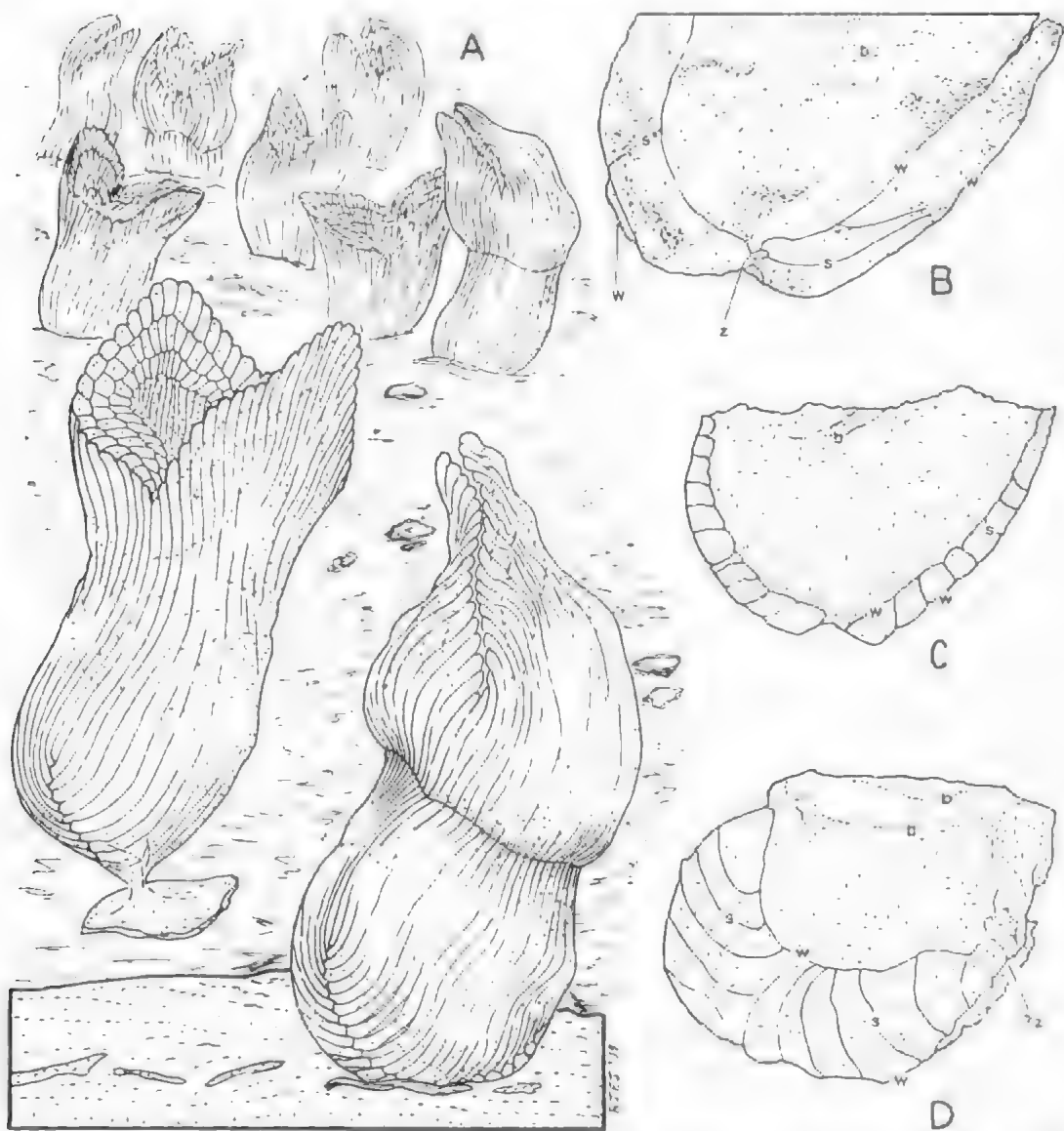


Fig. 6. *Ernieella plateauensis* Pflug, 1966. A, reconstruction of group of individuals living on sandy Precambrian sea bottom. Several possible alternative, but not necessarily mutually exclusive, reconstructions of individuals shown. Youthful specimens evidently attached to mud galls or other prominences on sea bottom, more mature specimens may have lived with basal parts buried in substrate. Outermost membrane seems to have been caul-like and only faintly showing underlying longitudinal structure. "Mouth" sometimes preserved broadly flared, or more frequently collapsed or pursed. Individuals of all sizes may show enigmatic transverse suture or possible zone of "budding" at about half their length. About .7 natural size. B-D, sketches of sectional cuts through actual specimens: b, traces of bedding in matrix (impure sandstone or quartzite); r, adhering thin shiver of rock; s, septal membranes evidenced by surfaces of parting or thin limonite stained traces; w, similarly evidenced wall membranes; z, known or inferred position of basal zig-zag suture; all $\times 1.5$. B, sublongitudinal section almost normal to zig-zag axis, three wall membranes evidenced. Pf. No. 120. C, section of another specimen almost transverse to longitudinal surface markings. D, section of different specimen cut oblique to longitudinal surface markings.

fissure fillings. In the present structures from the Flinders Ranges, however, the frequently fine lamination of the more silty phases of the infilling shows no evidence of disruption other than slight deformation during compaction, and the thin sand beds which often occur at the base of the cylinder show no sign of fissuring or disruption such as might be expected with the rapid escape of fluids. Thus our structures were evidently not formed by the upward escape or flowage of pore fluids. Also, the syngenesis of these structures eliminates an epigenetic concretionary origin. Such syngenetic structures could, therefore, only be formed inorganically as toroids or pot-casts; these names both essentially referring to the casts of circular scour pits.

In past literature, such scour pits are often suggested to have been formed by whirlpool action generated along the boundary between currents flowing in opposite directions. As such they might be expected to occur in high energy shallow-water environments in both marine and non-marine realms. According to Conybeare & Crook (1968), circular toroids are usually wider than deep. The external morphology of their casts is suggested to be characteristically swirled, like that of a "folded bun", generally with a smooth surface, although the formation of roughly concentric patterns by scouring is common. Internally, toroid casts may display structural and textural homogeneity.

Our structures show a marked resemblance to the "rippled toroids" described by Dorr & Kauffman (1963) from the Mississippian Napoleon Sandstone of southern Michigan. They considered these toroids to have been "formed by the action of vortex currents on unconsolidated sand in shallow water of the inner sublittoral zone" and supported their findings by inducing vortices in a water-filled, sand-floored box and producing artificial toroids. Some of the structures they described were elongate, oblique cones, a shape occasionally shown by our material.

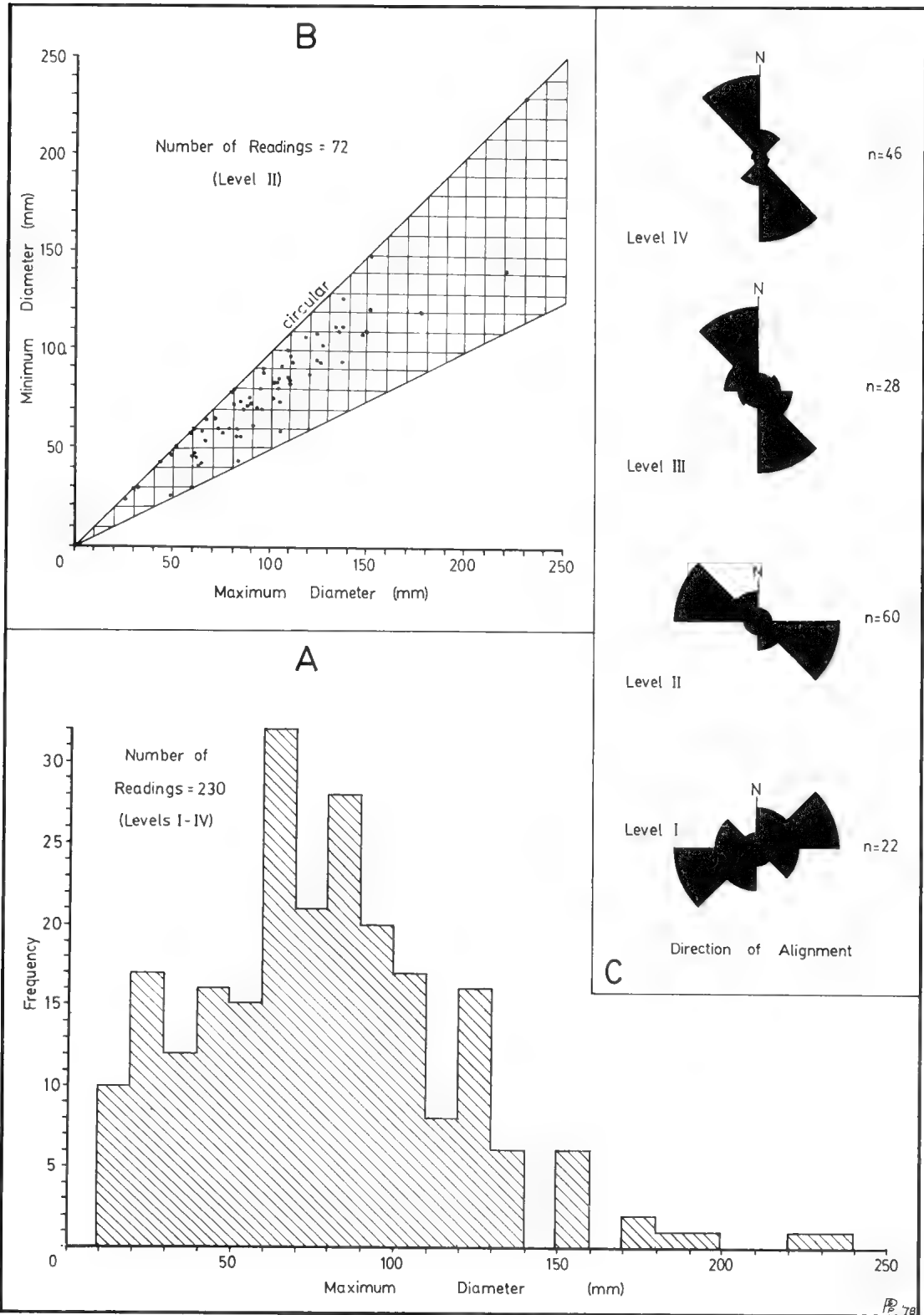
This precise explanation seems inapplicable with respect to our structures for several reasons. Dorr & Kauffman considered that the environment of deposition of the Napoleon Sandstone was one of relatively high energy and this is consistent with the texture of the rock (sand). Our structures occur within a variety of lithotypes representing mud to fine sand grades, reflecting microenviron-

ments of varying energy levels, and presumably mostly of rather low energy. The vortex hypothesis invoked by these authors implies tidal shear or near-shore phenomena which, by their very nature, must be restricted to a relatively narrow belt parallel to the palaeo-coast. We, however, have located our structures at geographic separations of 20 km parallel to the inferred depositional strike and perhaps 60 km at right angles to it. Also, our forms occur at various levels over a total stratigraphic thickness in excess of 1400 m.

Aigner & Futterer (1978) and Aiger (1978) document and explain inorganic pot-casts and gutter-casts from the Muschelkalk of southwest Germany. Some of the pot-casts which they figure (i.e. Aigner & Futterer 1978, figs. 3A, A¹, D, D¹ and E) are identical in shape and internal layering to the Flinders Ranges specimens, except that the coarse material at the base of the "pots" consists of shell debris rather than clay galls. The Muschelkalk pots may be packed within an edgewise conglomerate of shells similar to the edgewise conglomerate of mud flakes present in some of our specimens (Fig. 4G).

On the basis of flume experiments Aigner & Futterer attribute the Muschelkalk pot-holes to the erosive effects of eddy currents forming in shell-filled depressions due to the influence of a steady or increasing unidirectional current over the general surface of the substrate. They note that such pots are unknown on present-day tidal flats and consider that their origin is entirely submarine. The implications of this are at some variance with Plummer's (1978) finding that on the basis of such structures as flat-topped ripples, interference ripples and shallow channels with ebb-orientated asymmetric ripples, parts of the Moorillah Formation in which our structures occur frequently accumulated in a low intertidal mud flat environment. However, we did not observe any sedimentological structures in direct association with the pot-casts that would imply emergence.

An attractive aspect of this explanation for the Flinders Ranges structures is that sometimes the pot-casts are peculiarly coalesced or joined by uneven trough-like forms (Fig. 4B) which are exactly paralleled in the Muschelkalk material (Aigner & Futterer 1978, figs. 3B, C and F). In rare instances there may even be evidence of a ripple hollow or other depression in which the clay galls that



formed the erosive tools may have originally accumulated (Fig. 3A).

Measurements of the diameter of the pot-casts in the Flinders Ranges (Fig. 7A & B) show a range of variability quite comparable to gutter-casts studied by Aigner & Futterer and the depth of specimens is similar. A histogram of diameter against frequency (Fig. 7A) shows a somewhat skewed distribution with the modal diameter at 6–7 cm. A suggestion of a polymodal component in this histogram probably reflects the observation that specimens of the pot-casts on given bedding planes tend to be closely similar in size, a likely indication of their nearly simultaneous generation. Karez *et al.* (1974) describe how a field of small pits (individually reaching up to 9 mm diameter) may form on freshly deposited clay under the influence of a current, and it may be possible that such depressions serve as a nucleus for the subsequent formation of pot-holes.

The study of Aigner & Futterer also demonstrates a very marked preferred orientation for the Muschelkalk gutter-casts, parallel to the coastline and basin axis. Our pot-structures are usually ovoid in outline (Fig. 7B) and measurements on four bedding-planes in ascending stratigraphic order at Utanouna Creek also demonstrate a marked preferred orientation for any given bedding plane (Fig. 7C), though this direction changes by 90° between the lowest and the third surfaces studied. The more or less east-west orientations for Levels I and II are approximately normal to the palaeodepositional trends for the Flinders Ranges area, whilst the N.N.W. S.S.E. directions for Levels III and IV are roughly parallel to the basin axis and (western) shoreline (e.g. see Plummer 1978).

The individual pot-casts are spaced on bedding planes at intervals of several tens of centimeters to several meters. In rare instances specimens are grouped on part of a bedding plane, while none are present on the remainder of the surface. Dorr & Kaufman (1963) pointed out that the "rippled toroids" which they described also show a patchy distribution. Similarly Norrman (1964) indicated a

clumped distribution for modern day pot-holes eroded into a clay lake bottom.

Associated pseudofossils and oldest local record of metazoans

Glaessner (1969) described the complex trace-like marking *Bunyerichnus dalgarnoi* from the base of the presently recognised Moorillah Formation at Bunyeroo Gorge. He considered that this marking may have been made by an animal related to a primitive mollusc without a shell. Large bedding plane exposures are a persistent feature of many outcrops of the Moorillah Formation at this locality, but despite extensive searches no new finds of *B. dalgarnoi* have been made during the decade since its discovery. After critical examination of *B. dalgarnoi*, Jenkins (1975a) suggested that it is a composite of primary impressions occurring on two separate bedding planes, and thus unlikely to be of metazoan origin. The great frequency with which inorganic tool markings occur in this formation led Jenkins to consider it to be "a unique accidental set of markings made by a tethered implement moved by the current". The implement may have been a small mud clast caught in a tassel of twisted algal threads. It is suggested to have moved in a series of small jumps in several arcuate swaths to leave overlapping, curved bands of more or less regular, transverse imprints marking successive bedding planes. Thalys-bearing, ribbon-like algae, which might have provided the tether, appear in the Riphean of the U.S.S.R. and form accumulations grading into supropelic laminae and films in the Vendian (Sokolov 1977).

Small circular markings on a bedding plane of a single loose block of rock found within the Moorillah Formation have been considered as structures formed by escaping gas (Plummer 1980).

The oldest probable record of metazoans in the Flinders ranges is of markings resembling small medusoids and fine sinuous trails found by Dr Mary Wade at Brachina Gorge within the Bonney Sandstone (previously the "Red Pound Quartzite") which is the lower formation of the Pound Subgroup (Wade 1970, p.

Fig. 7. Measurements of pseudofossils at Utanouna Creek, Bimbinyunna Range. A, histogram of maximum transverse diameter of specimens plotted against frequency; specimens occur on four large bedding planes, levels I–IV in ascending stratigraphic order. B, plot of maximum and minimum transverse diameters of individual specimens occurring on level II. C, direction of orientation of longer transverse axis of ovate specimens plotted for each bedding plane.

92). Other finds of Precambrian metazoans in Australia are apparently either approximately equivalent in age to the Ediacara assemblage *sensu stricto*, or are likely of younger age as is inferred for the Mt Skinner "fauna" of the Amadeus and Georgina Basins (see Wade 1969; Daily 1972; Kirschvink 1978). It thus becomes timely to consider why the several thousand metres of Marinoan or youngest Precambrian sediments which precede the Pound Subgroup in the Flinders Ranges, and which are well exposed and otherwise occur extensively throughout the Adelaide Fold-Belt, are apparently barren of metazoan fossils. Numerous stratigraphical and sedimentological studies generally imply marine origins for much of this succession (Thomson 1969; Thomson *et al.* 1976; Plummer 1978). Arguments that the facies may not have been suitable for the preservation of small soft-bodied remains (cf. Glaessner 1972) are not fully convincing as finely laminated beds preserving the smallest inorganic tool-markings (ca. 0.5 mm) are frequent, and Wade (1968, 1970) has found that the conditions needed for the preservation of a soft-bodied assemblage were not particularly stringent. Indeed the Ediacara assemblage *sensu lato* is now known to occur in quite variable facies at different World localities.

An extensive literature concerns supposed finds of either body fossils or trace fossils predating the Ediacara assemblage *sensu lato*, but subsequent studies have led frequently to a questioning of the interpretation or sometimes the age of these reported occurrences (Glaessner 1969, 1979 and pers. comm.; Cloud 1973, 1978; Cloud *et al.* 1980; Sokolov 1977; Yakobson & Krylov 1977). Other of these finds continue to be cited as possible evidence supportive of ideas of a gradualistic evolution of early metazoans (e.g. Glaessner 1972, 1979; Bengtson 1977; Brasier 1979). The studied record of the sequences in the Flinders Ranges does not provide evidence of an extended early history for the metazoans.

Rather negative evidence and the known occurrence of fossils in the Flinders Ranges lend support to ideas such as those of Stanley (1973, 1976a, 1976b) suggesting a late radiation of metazoans, predicted on a basis of ecological modelling, or to an exponential increase in animal life from the late Precambrian to the Cambrian, shown by analysis of age data and counts of recognized taxa (Sepkoski

1978, 1979). Stanley considered that the early radiation of eukaryotes may have been inhibited by the saturation effect of Precambrian algal systems and suggested that the advent of cell-eating heterotrophy triggered a "kind of self-propagating feedback system of diversification" culminating in the initial major radiations of both the metaphytes and metazoans.

Recently Choubert & Faure-Muret (1980) assigned a middle Riphean age to the rocks containing Precambrian metazoan fossils on the Avalon Peninsula, Newfoundland, and at Charnwood Forest, England. This finding is patently incorrect, and not only overlooks lines of geological evidence which suggest that these rocks are late Precambrian (Williams & King 1979; Patchett *et al.* 1980), but ignores a 20 year cycle of research documenting Vendian or Ediacaran affinities for the genera *Charnia* Ford and *Charniodiscus* Ford present in the fossil assemblages (Glaessner 1977, 1979).

Conclusions

The present study describes Precambrian structures which have a relatively complex genesis and show resemblances to certain cylindrical to conical fossil burrows, as well as to sack-shaped, longitudinally striate body fossil remains of comparable age. However, these resemblances appear to be fortuitous and the true origin of the structures is suggested to be as erosive pits formed by vortices induced by episodic currents and the scouring action of trapped mud galls. The hydrodynamic conditions leading to their formation are not fully understood and to our knowledge no such structures have yet been described from present day, marine, sub-tidal environments. The degree of resemblance between these pseudofossils and several burrow forms and sack-shaped body fossils emphasizes that a variety of both inorganic and organic processes may lead to the formation of closely similar structures which may even show degrees of gradation. The corollary of this finding is that the description of such kinds of Precambrian structures and the assignment of a particular genesis, especially one of biological origin, should be approached with caution.

The finding of these structures and recognition of other associated pseudofossils suggests that true indications of Metazoa are restricted to the highest part of the local

Precambrian sequence, thus providing negative evidence supporting recent theories that postulate a late evolution or radiation of animal life towards the close of the Precambrian.

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SONDEROPHYCUS AND THE TYPE SPECIMEN OF PEYSSONNELIA AUSTRALIS (CRYPTONEMIALES, RHODOPHYTA)

BY *H. B. S. WOMERSLEY & D. SINKORA*

Summary

The type specimen of *Peyssonnelia australis* Sonder in MEL is a *Peyssonnelia* and is distinct from the taxon known as *Sonderophycus australis* (Sonder) Denizot. The latter, which is based on *P. australis* Sonder, is distinct generically from *Peyssonnelia* and is therefore re-described as *Sonderopelta coriacea* gen. et sp. nov. *P. australis* Sonder is an earlier name for *P. gunniana* J. Argadh but a synonym of *P. capensis* Montagne.

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by H. B. S. WOMERSLEY* & D. SINKORA†

Summary

WOMERSLEY, H. B. S. & SINKORA, D. (1981) *Sonderophycus* and the type specimen of *Peyssonnelia australis* Sonder (Cryptonemiales, Rhodophyta). *Trans. R. Soc. S. Aust.* **105**(2), 85-87, 12 June, 1981.

The type specimen of *Peyssonnelia australis* Sonder in MEL is a *Peyssonnelia* and is distinct from the taxon known as *Sonderophycus australis* (Sonder) Denizot. The latter, which is based on *P. australis* Sonder, is distinct generically from *Peyssonnelia* and is therefore re-described as *Sonderopelta coriacea* gen. et sp. nov. *P. australis* Sonder is an earlier name for *P. gunniana* J. Agardh but a synonym of *P. capensis* Montagne.

Introduction

Peyssonnelia australis Sonder (1953, p. 685) has been recently referred to as *Sonderophycus australis* (Sonder) Denizot (1968, pp. 260, 307). Earlier it had been referred to as *Ethelia australis* (Sonder) Weber van Bosse (1921, p. 300), though Weber van Bosse's record "Archipel Indien" seems likely to apply to a different taxon. The description of Denizot was probably based on material such as that illustrated by Harvey (1859, pl. 81), and this is indeed a distinctive southern Australian species.

However, the type specimen of *P. australis* Sonder in MEL (573182) is not the plant now known as *Sonderophycus australis* but is *Peyssonnelia gunniana* J. Agardh (1876, p. 387), which Denizot (1968, p. 123) places as a synonym of the South African *P. capensis* Montagne (1847, p. 177).

The type specimen of *P. australis* in MEL, from Holdfast Bay, South Australia (*F. Mueller*), includes a small sheet with Sonder's handwritten notes on both sides; several phrases are repeated in the type description. This number, with four pieces of thallus in an envelope, is regarded as the holotype. There is a further specimen in MEL (573183) labelled by Ferdinand Mueller and which is probably isotype material. Sonder later also included some *Sonderophycus* specimens under his *P. australis*.

P. australis Areschoug (1854, p. 352) from "sinu Port Adelaide" (specimens in S) is the same as Sonder's type; Areschoug's name was apparently independent of Sonder's.

It seems likely that all references to *Sonderophycus* or its synonyms apply to this genus as understood by Denizot, apart from Sonder's original description. The misinterpretation of Sonder's type probably dates from Harvey's 1859 description and his Alg. Aust. Exsicc. 328E from Port Phillip Heads, Vic. (also Harvey, Trav. set 434 from the same locality).

Since the generic name *Sonderophycus* is based on *Peyssonnelia australis* Sonder, it must be relegated to synonymy of the latter. No alternative generic name or specific epithet exists for *Sonderophycus*, which dates only from 1968 and was imperfectly presented (Denizot did not see and failed to cite the full date for Sonder's publication, viz. 18. . for 1853, and the French discussion and citation of basionym are given on p. 260 with the latin diagnosis on p. 307).

Accordingly this distinctive taxon is here described as a new genus and species.

Sonderopelta coriacea gen. and sp. nov.

Peyssonnelia australis sensu Harvey 1859: pl. 81.

NON *P. australis* Sonder 1853: 685.

Ethelia australis? (Sonder) W.v. Bosse 1921: 300.

Sonderophycus australis (Sonder) Denizot 1968: 260, 307.

Sonderopelta gen. nov.

Thallus uncalcified, with a short, thick and felty stipe of entangled rhizoids and an extensive relatively thick and cartilaginous lamina extending eccentrically from the stipe position with concentric growth zones, variously lobed and lacerate; lamina in section composed of radiating filaments of cells of similar size, spreading both to the underside of the thallus with frequent terminal cells of the filaments

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Fig. 1. The holotype specimen of *Sonderopelta coriacea*.

producing attachment rhizoids, and to the upper (light-facing) surface with the filaments becoming erect and short celled to form the cortex. Reproduction unknown.

Thallus non calcareus, stipite rhizoideorum brevi et crasso et lamina extensiva crassa cartilaginea a positione stipitis zonis concentricis auctus eccentricae extensa, lobata vel lacera; lamina in sectione e filamentis radiatis cellularum amplitudinis similis composita, filamenta utrinque extendentia, ad paginam inferiorem cellulis frequentibus terminalibus filamentorum haptera efferentibus, ad paginam superiorem filamentibus erectescentibus et cellularibus brevis cortex formantibus. Reproductio incognita.

Type species. *S. coriacea* sp. nov.

S. coriacea sp. nov.

Thallus (Fig. 1) eccentrically peltate, spreading from a short (to 2 cm long and

1½ cm broad), fibrous and often divided stipe, usually growing under overhangs in low light intensity; lamina cartilaginous, ½-1 (-1½) mm thick, radiating eccentrically from the stipe, often deeply divided or lacinate with lobes to 20(-25) cm long and to 15 cm broad, margin smooth, convex to rounded, dark red-brown above (side to light), grey and fibrous (from septate rhizoids) below where in larger plants this side is ½-2 cm from the rock substrate.

Thallus eccentricae peltatus, ab stipe (ad 2 cm longo et 1½ cm diametro) breve saepe diviso patens, plerumque sub petra imminente in luce demissa vivens; lamina cartilaginea, ½-1 (-1½) mm crassa, a stipe eccentricae radians, saepe divisa profunda vel laciniata lobis ad 20(-25) cm longis et ad 15 cm latis, margo laevis, convex ad circularis, pagina ad lucem superior sanguinea, pagina inferior cinerea fibrosa (per rhizoidea septata) in plantis magnioribus ½-2 cm a substrato.

Type locality: Pandalowie Bay, Yorke Peninsula, S. Aust. (2-3 m deep in shade, 14.ii.1981; S. M. Clarke).

Type: ADU, A52035 (Fig. 1). Isotypes to be distributed as No. 214 in "Marine Algae of southern Australia".

Sonderopelta is named to commemorate Otto Wilhelm Sonder (1812-1881), combined with the peltate form of the well-developed thallus.

Distribution: From the Isles of St Francis, S. Aust. to Waratah Bay, Vic. and around Tasmania, mainly on rough-water coasts in depths of 1-25 m, usually in heavy shade.

Sonderopelta differs from *Peyssonnelia* in thallus structure, having longitudinal filaments which diverge to both upper and lower surfaces, whereas *Peyssonnelia* has a distinct basal hypothallial layer producing filaments above and attachment rhizoids below. *Ethelia*, in which *Sonderopelta* was placed with some doubt by Weber van Bosse, differs in having upwardly and downwardly directed filaments produced from a central, apparently limited, layer of distinctly larger filaments; it also differs in being fully adherent to the substrate but without producing attachment rhizoids.

Peyssonnelia australis Sonder

Peyssonnelia australis is a common subtidal alga on southern Australian coasts. *P. gunniana* J. Agardh (1876, p. 387), based on a collection of Harvey (3271) from George-

town, Tasmania (type in Herb. Agardh, LD, 27698) which had been earlier referred to the European *P. rubra* Harvey, becomes a synonym of *P. australis*, and *P. coccinea* J. Agardh (1876, p. 385) from Western Australia (probably near Bunbury) (type in Herb. Agardh, LD, 27650) is probably also synonymous.

Denizot (1968, p. 123) placed *P. gunniana* as a synonym of *P. capensis* Montagne (1847, p. 177) from South Africa (type in PC?) but without detailed comments on their identity. Denizot regarded the presence of internal calcified granules as well as hypobasal calcification as characteristic of *P. capensis* (as well as other features such as the septate rhizoids), and Australian specimens appear to be specifically identical with ones studied from South Africa (e.g. Isaac 307 from Terguict, near Mossel Bay, 13.x.1954; ADU, A40825).

Hence *P. australis* Sonder should be regarded as a synonym (along with *P. gunniana* J. Agardh) of *P. capensis* Montagne.

Acknowledgements

We are grateful to Dr Paul Silva and Dr Jim Ross for comments on nomenclatural aspects, and to Mr S. A. Shepherd and Mr S. M. Clarke for comments on the growth habit and habitat of *Sonderopelta*. Dr E. M. Gordon-Mills kindly supplied the latin diagnoses.

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PARTIAL ACQUISITION OF PIGMENTATION IN AN ADULT, ALBINO, AUSTRALIAN LEPTODACTYLID FROG (LIMNODYNASTES DUMERILI PETERS)

BY MICHAEL J. TYLER AND MARGARET DAVIES

Summary

Although there are sporadic reports of the discovery of albino frogs, the individuals involved generally are stable in their lack of pigment. Exceptions are the observations of European *Rana* species in which the tadpoles derived from albino ova acquired normal pigmentation gradually over a period of approximately two weeks. We have not located the description of pigmentation developing in albino frogs in later stages in their ontogeny.

BRIEF COMMUNICATION

PARTIAL ACQUISITION OF PIGMENTATION IN AN ADULT, ALBINO, AUSTRALIAN LEPTODACTYLID FROG (*LIMNODYNASTES DUMERILI* PETERS)

Although there are sporadic reports of the discovery of albino frogs, the individuals involved generally are stable in their lack of pigment. Exceptions are the observations¹⁻⁴ of European *Rana* species in which the tadpoles derived from albino ova acquired normal pigmentation gradually over a period of approximately two weeks. We have not located the description of pigmentation developing in albino frogs at later stages in their ontogeny.

On 22.8.79 we received a gravid female *Limnodynastes dumerili* collected at Evanston near Gawler, South Australia. The body was dull pink with darker areas on the flanks where the internal organs could be seen in partial transparency through the body wall. The eyes were pigmented normally and for this reason, conform to the description of "partial albino" frogs in the terminology of Pavese⁵, Smallcombe² and Dubois⁶.

The female was placed with a group of normally pigmented *L. dumerili* from North Adelaide. On 22.9.79 she mated with one of the normal males and laid approximately 3,100 pigmented eggs of which 1,170 were infertile. The tadpoles were pigmented normally, and the resultant metamorphosing frogs were perfectly normal in external appearance and behaviour. A very high death rate in the offspring following metamorphosis was attributed to overcrowding at a time when competing requirements for other research animals limited the space available for them. Ten individuals remained in October 1980, but they were relatively small (snout to vent length 35 mm), and they died over the following three months.

In November 1980 the female began to acquire a few small (3 mm diam.), circular spots of black pigment. Initially these were confined to the skin covering the tibial glands, and the pigment areas expanded there until each gland was pigmented entirely. Over a period of several months a dark mosaic of pigment then developed upon the



Fig. 1. Partial albino *Limnodynastes dumerili* Peters.

dorsum and limbs (Fig. 1), so producing a piebald appearance. Unfortunately the female died before pigmentation had extended further. At death her snout to vent length was 66 mm which is within the normal range for the species.

We have been unable to trace in the literature other examples of the delayed acquisition of pigmentation comparable to that reported here. Certainly it is a normal event for many frog species to change colour and markings in the course of their early ontogeny, but the changes reported here occurred at a post-reproductive stage.

In our search for records of comparable phenomena in other vertebrates, it has become apparent that the term "partial albinism" as employed for frogs by Pavese⁵, Smallcombe² and Dubois⁶ has a different interpretation to the "partial albinism" of mammals exhibiting the Chediak-Higashi Syndrome (CHS) reported by other authors⁷⁻¹⁰. CHS is characterized by a paucity of pigment of the eyes and skin (or hairs), as opposed to lack of pigment in the skin and presence in the eyes.

We thank Chris Miller for assistance with the rearing of the tadpoles.

¹Smallcombe, W. A. (1938). *Nature* 141 (3573), 753.

²— (1949). *J. Genet.* 49, 286-90.

³Rostand, J. (1946). *Anoures Rev. Sci.* 84, 564-5.

⁴Sladeczek, F. (1964). *Folia Biol. (Prague)* 10, 23-9.

⁵Pavese, P. (1879). *Rend. 1st Lomb.* 2, 528-34.

⁶Dubois, A. (1979). *Mitt. Zool. Mus. Berlin* 55, 59-87.

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Transactions of the Royal Society of South Australia Incorporated

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TAXONOMY AND ECOLOGICAL NOTES OF SOME OSTRACODS FROM AUSTRALIAN INLAND WATERS

BY P. DE DECKKER

Summary

Two new ostracod genera *Alboa* and *Gomphodella* are described and 11 new species: *A. worooa*, *Bennelongia barangaroo*, *B. pinpi*, *B. nimala*, *Australocypris dispar*, *Strandesia phoenix*, *Reticypis clava*, *R. kurdimurka*, *Ilyocypris perigundi*, *Leptocythere lacustris*, and *Gomphodella maia*. Ecological notes are presented for these and an additional eight species, some of which are re-described.

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Summary

DE DECKKER, P. (1981) Taxonomy and ecological notes of some ostracods from Australian inland waters. *Trans. R. Soc. S. Aust.* 105(3), 91-138, 11 December, 1981.

Two new ostracod genera *Alboa* and *Gomphodellella* are described and 11 new species: *A. worooa*, *Bennelongia baranganoo*, *B. pinpi*, *B. nimala*, *Australocypris dispar*, *Strandesia phoenix*, *Retiocypris clava*, *R. kurdimurka*, *Hyocypris perigrandi*, *Leptocythere lacustris*, and *Gomphodellella maia*. Ecological notes are presented for these and an additional eight species, some of which are re-described.

Introduction

Ostracods are common inhabitants of most types of waterbodies in Australia with the halobiont fauna being particularly diverse here compared to other parts of the world (De Deckker 1981). However, taxonomic knowledge of Australian ostracods is incomplete, as indicated by the numerous ostracods referred to in open nomenclature in publications dealing with limnological surveys. The present paper sets out to describe some of the common ostracod species found in inland waters by providing many illustrations of their shell to simplify further identifications.

The specimens used for the descriptions here are deposited at the South Australian Museum.

Systematic descriptions

SUBCLASS: OSTRACODA Latreille, 1806

ORDER: PODOCOPIDA Müller, 1894

SUPERFAMILY: CYPRIDACEA Baird, 1845

FAMILY: CYPRIDIDAE Baird, 1845

SUBFAMILY: CYPRINOTINAE
Bronstein, 1947

Alboa n.gen

Type species: *Alboa worooa* n.sp., gender masculine.

Diagnosis: Asymmetrical valves: in anterior view, greatest width of right valve at 0.5 from dorsum and of left valve at 0.7 from dorsum. Selvage prominent in left valve and placed at 0.5 of width of inner lamella anteriorly. Peripheral groove on the outside of selvage in left valve.

Male maxillar palps strongly asymmetrical; lateral lobe and distal part of copulatory sheath boot-shaped. Geniculate joint between 1st and 2nd thoracopoda I segments with two unequal setae.

Derivation of name: *Alboa* meaning egg in aboriginal language to refer to the egg-shaped shell.¹

Alboa worooa n.sp.

FIGS 1-2

1919 Cypris sydneya King: Chapman, p. 27

Diagnosis: As for genus.

Description: *Carapace* (External). Pseudopunctate, oval-shaped with ventral area almost flat except in mouth area which is slightly concave at about 0.4 from anterior. In left valve, other faint concavity, anterior to mouth region at about 0.2 from anterior. Greatest height and width at about middle. Left valve larger and overlapping right one anteriorly, posteriorly and ventrally. In anterior view, valves strongly asymmetrical; left valve, broader and larger; greatest width of left valve at 0.7 from dorsum and of right valve at 0.5 from dorsum. Carapace pilose with a few long hairs in posterior area. Flange broadest in left valve. Normal pore canals simple and rimmed. (Internal). Inner lamellae broadest anteriorly and ventrally but slightly broader in left valve; posteriorly, inner lamella of right valve very narrow. In left valve, selvage prominent and at about 0.75 of inner lamella's width from outer margin. Selvage follows curvature of shell except anteriorly where it is less curved. Posteriorly, selvage less prominent and at about 0.5 of inner lamella's width. Peripheral narrow depression on outside of selvage. In right valve,

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¹ Aboriginal words used in this text are from Papps (1965) and Cooper (1962).

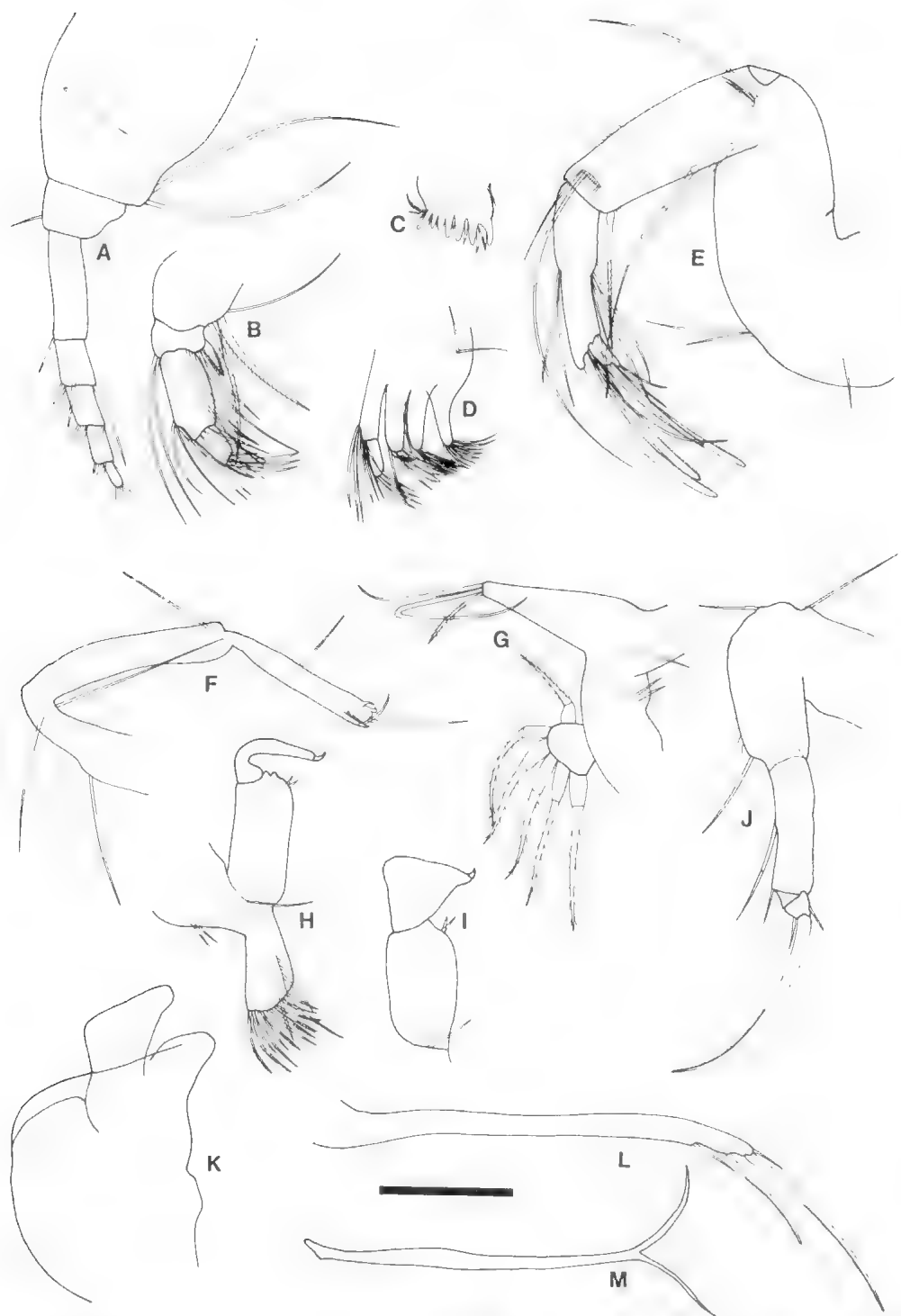


Fig. 1. *Alboa worooa* n.gen., n.sp. a antennula, b mandible—palp, c mandible—coxale, d maxillula, e antenna, f thoracopoda II, g maxilla, female, h maxilla, male, i maxilla—endopodite, male, j thoracopoda I, k hemipenis, l furca, m furcal attachment. a-e, h-m: holotype adult male. g: paratype: adult female. Scale: 100 μ .

selvage peripheral and faint except anteriorly where it is much sharper and extends further than edge of shell. Right valve with faint tubercles posteroventrally along edge of shell. Radial pore canals numerous, narrow and straight. Central muscle field consisting of three scars in front and two behind; upper and lowest scars in front broad and elongated whereas other two almost circular. Mandibular scars below and in front of central muscle field.

Anatomy. Antennulae: (Fig. 1a) 7-segmented; length-width ratio of last six segments: 2/3, 3/1, 1/1.4, 3/2, 1.75/1, 2.5/1. Most plumose natatory setae as long as all segments together.

Antennae: (Fig. 1e) No obvious sexual dimorphism; three long claws plus a smaller one; natatory setae reaching tip of claws.

Mandible: (Figs 1b,c) Mandibular coxale with seven teeth; last tooth longer than penultimate and near its base externally with three setae of different sizes; longest one pilose. Endopod with α bristle short, narrow and barren; β bristle thick, stout and tufted; γ bristle longer than terminal segment, thick and with short hairs on external side.

Rake-like organ: Six or seven short and stout teeth with an additional bifid one on inner side of each rake.

Maxillular: (Fig. 1d) 3rd lobe with top toothed Zahnborsten; length width ratio of both palps: 3/1.

Maxilla: Sexually dimorphic: in male, palps strongly asymmetrical with right one broader (Figs 1h,i). In female (Fig. 1g) endopod with three plumose setae; longest one in middle and two others of unequal length. In both sexes, epipod with five long plumose Strahlen and one shorter plumose one near base of plate.

Thoracopoda I: (Fig. 1j) Penultimate segment weakly divided. Two setae on geniculate joint between 1st and 2nd segment; anterior seta longest.

Thoracopoda II: (Fig. 1f) End of last segment with two unequal setae and terminal pincers.

Hemipenis: (Fig. 1k) Lateral lobe boot-shaped with base rather broad and inner distal end of copulatory sheath of similar shape to lateral lobe.

Zenker organ: Both ends rounded and with 40 rosettes.

Furca: (Fig. 1l) Pectinate claws unequal with posterior claw 0.7 of length of anterior one and anterior seta 0.17 of anterior claw, and shorter than posterior seta.

Furcal attachment: (Fig. 1m) Long and narrow with distal end bifurcate; ventral and dorsal branches of similar width and length.

Eye: Cups of nauplius eye fused; dark brown.

Colour of shell: green.

Size:

holotype adult male

	L	H		L	H
LV	1540 μ	880 μ	RV	1460 μ	860 μ

paratype adult female

	L	H		L	H
LV	1700 μ	1000 μ	RV	1640 μ	980 μ

Type locality: Pool on the southern side of Light River, 20 m from the bridge on the Port Wakefield Road, north of Adelaide, S.A. (34°33'09"S, 138°27'20"E).

Derivation of name: From the aboriginal language, *worooa* meaning green for the colour of the shell.

Ecology and distribution: *A. worooa* inhabits lakes and temporary pools. This species is found in fresh waters and its highest salinity record is 3.5‰ at the type locality. *A. worooa* has also been recorded from the following localities: roadside pool, 13 km east of Rocky River and Duck Lagoon, both on Kangaroo Island, S.A., and Granite pool at Newmann's Rocks, 140 km east of Norseman, W.A. Additionally, valves of this species have been found in subsurface sediments at Birchmore Lagoon, Kangaroo Island (in those specimens, the asymmetry of the valves is more pronounced with the right valve forming a broader hump dorsally). This species has also been described by Chapman (1919) as *Cypris sydneya* from Pleistocene (fide Chapman) sediments from Boneo Swamp near Cape Schanck, Vic.

Remarks: *A. worooa* is related to the *Heterocypris* species as their anatomy is similar, in particular the triangular shape of the right maxillar palp in the male and the boot-shaped lateral lobe of the hemipenis. The asymmetrical valves and the presence of faint tubercles on the edge of the valve are also similar to *Heterocypris* species. The major difference is the pre-

* LV, RV = left valve, right valve. L, H = length, height.

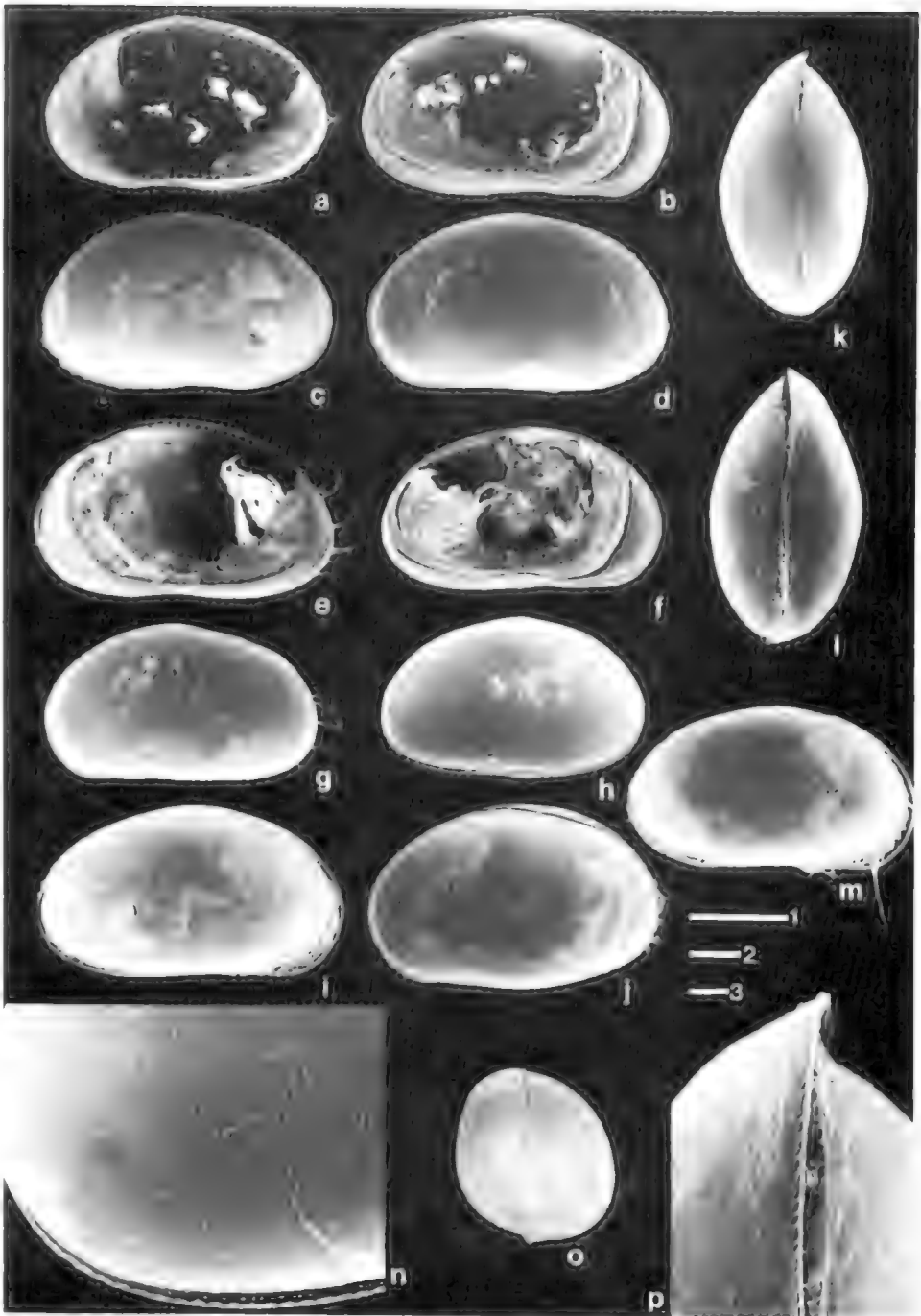


Fig. 2 *Alboa worooa* n.gen., n.sp. a RV internal, female paratype. b LV internal, female paratype. c RV external, female paratype. d LV external, female paratype. e RV internal, male holotype. f LV internal, male holotype. g LV external, male paratype. h RV external, male paratype. i C showing RV, female paratype. j C showing LV, female paratype. k C dorsal, male paratype. l C ventral, male paratype. m C showing RV, male paratype. n C showing RV, posterior detail of h. o C anterior, male paratype. p C dorsal, anterior detail of k. Scale: 1—500 μ for a-m; 2—50 μ for n; 3—50 μ for p. LV, RV = left valve, right valve. C = carapace. All views are lateral ones except when indicated.

sence of a prominent selvage in *A. worooa* not seen in *Heterocypris* species nor in the closely allied species grouped in *Cyprinotus*. This feature of the shell is sufficient to warrant separate generic distinction. Additionally, the right valve of *A. worooa* is not curved outwards in the anterior area compared to *Heterocypris* and *Cyprinotus* species.

SUBFAMILY: CYPRIDINAE Baird, 1845

Bennelongia De Deckker & McKenzie, 1981

Type species: Bennelongia harpago De Deckker & McKenzie, 1981

Remarks: *Bennelongia* comprises five Australian species: *B. harpago* De Deckker & McKenzie, 1981, *B. australis*, *B. barangaroo* n.sp. (= *Chlamydotheca bennelong* (King) *sensu* Sars 1894, 1896), *B. nimala* n.sp., *B. pinpi* n.sp. It is likely that *Strandesia feuerborni* Klie, 1932 and *Strandesia flavescens* Klie, 1932, both described from Indonesia, belong to *Bennelongia*. From the original description and illustrations of the valves (Klie 1932), it appears that these two species are characterized by the asymmetrical valves so typical of *Bennelongia* species. Two specimens resembling *S. feuerborni* have been collected from Cauckingburra Swamp, at Lake Buchanan, S.W. of Charters Towers, Queensland. One specimen is illustrated in Fig. 9r but no further identification has been carried out.

Bennelongia australis (Brady, 1886)

1886 *Chlamydotheca australis* n.sp., Brady, p. 91. *Diagnosis:* Area just behind the beak-like feature of the left valve strongly concave and outline of hemipenis as in Figs. 6f,j.

Description: *Carapace.* (External) Adult: Pseudopunctate and pilose carapace, oval with flattened ventrum and concave mouth region. Asymmetrical valves: left beak-shaped anteroventrally with deeply concave depression posterior to beak. Right valve almost smoothly curved anteroventrally except for narrow beak-like flange there. This flange overlapped by beak-like anterior area of left valve when carapace closed. In dorsal view, carapace egg-shaped with both valves slightly pinched laterally at about 0.17 from anterior. Simple type normal pore canals. Bordering edge of right valve anteriorly are a number of small quadrate tubercles.

Juvenile: Ellipsoidal to subtriangular in shape; symmetrical valves without beak-like feature,

and surface of shell either deeply pitted or coarsely reticulated with large wart-like tubercles present mostly anteriorly and posteriorly. Reticulation especially varied in smallest juveniles with some large sieve-like plates.

(Internal) Adult: Inner lamellae broader anteriorly than posteriorly. In left valve, selvage narrow but distant from inner margin posteriorly and ventrally; anteroventrally inner list forms broad but short lip-like flap which is absent anterodorsally. Deep depression anterodorsally near edge of shell and following curvature of inner margin anteriorly. It is absent in vicinity of lip-like flap. No outer list in left valve. Right valve with selvage peripheral except in anteroventral area where it is slightly broader and further inside inner lamella. Behind mouth region, flange thin but broad, and curves outward to almost reach tubercles. Outer list faint, running parallel to curvature of shell bordered with tubercles in front of mouth region and posteroventrally. Radial pore canals narrow and straight. Central muscle field consists of broad horizontal scar above, two parallel ones below and another broad one behind. Two additional, almost circular scars, one behind middle posterior one and other behind bottom scar. Two broad mandibular scars in front and below.

In juveniles, inner lamellae of similar width all around except in posteroventral area where they are slightly broader. Selvage broad, following curvature of shell and with no lip-like flap. Flange narrow but obvious in both valves and of same width as outer list which runs parallel to curvature of shell. Depression caused by some wart-like tubercles on outside area are seen inside valves.

Anatomy. Antennula: (Fig. 6a) Natatory setae as long as all the segments together. Length/width ratios of the terminal six segments are: 1/1, 5/2, 1.8/1, 2/1, 2.3/1, 2/1.³

Antenna: (Fig. 6d) Natatory setae extend to tip of claws. Three claws plus shorter one in both sexes; one of additional short and thin claw attached to terminal segment in male is longer and denticulated in female.

Mandible: (Fig. 6b) Mandibular coxale with seven teeth; endopod with long, narrow and barren α bristle, thick, stout and pilose β bristle and long pilose γ bristle which is twice as long as last segment.

³ The ratios of the 6 segments of *B. harpago* have been inverted in the original description.

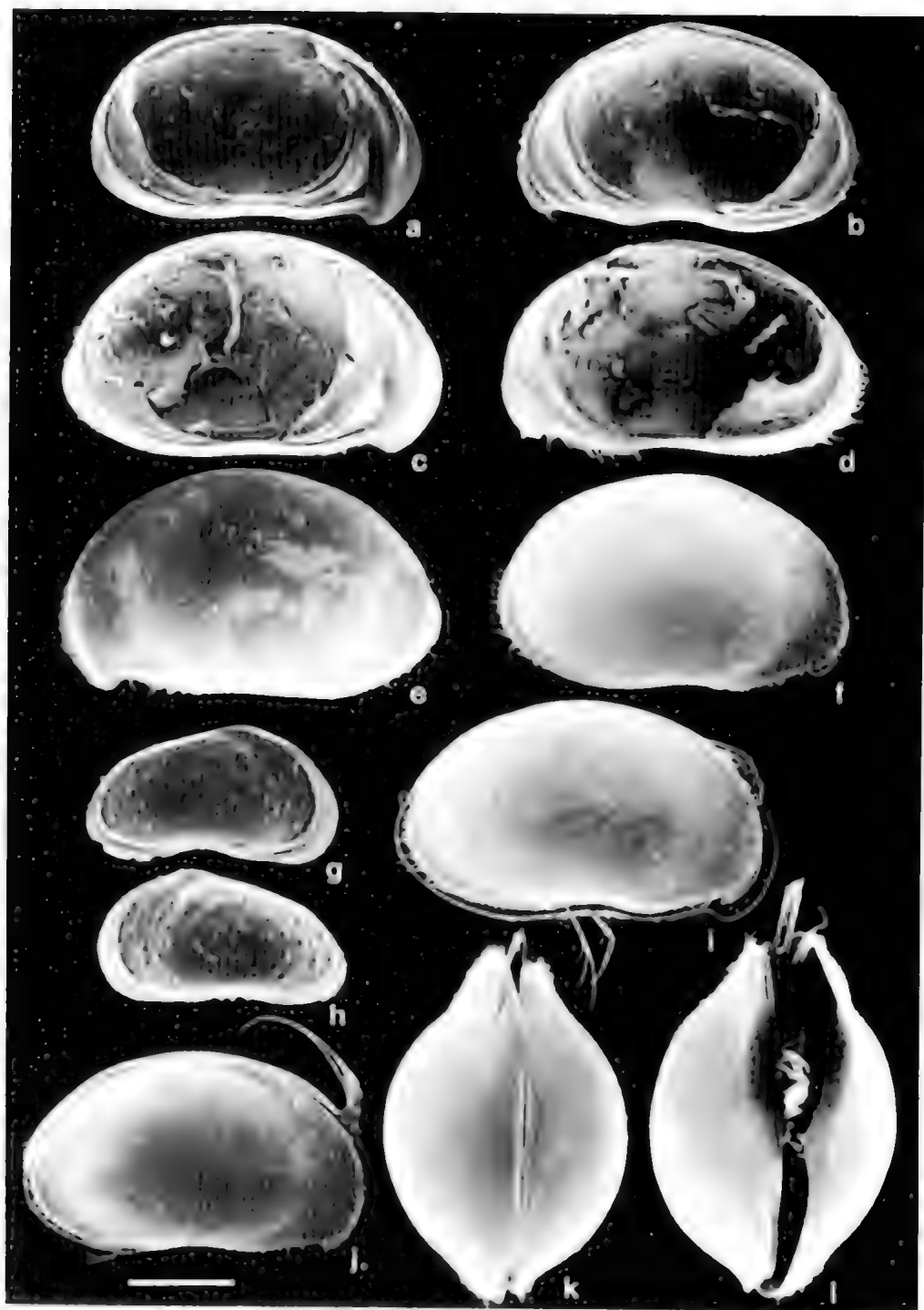


Fig. 3. *Bennelongia australis* (Brady, 1886) n.gen. a LV internal, male. b RV internal, male. c LV internal, female. d RV internal, female. e LV external, female. f RV external, female. g LV internal, juvenile. h RV internal, juvenile. i C showing RV, female. j C showing RV, male. k C dorsal, female. l C ventral, female. a-l: Creek pool flowing across the road, 2 km N of Leonora, W.A. Scale: 500 μ m.

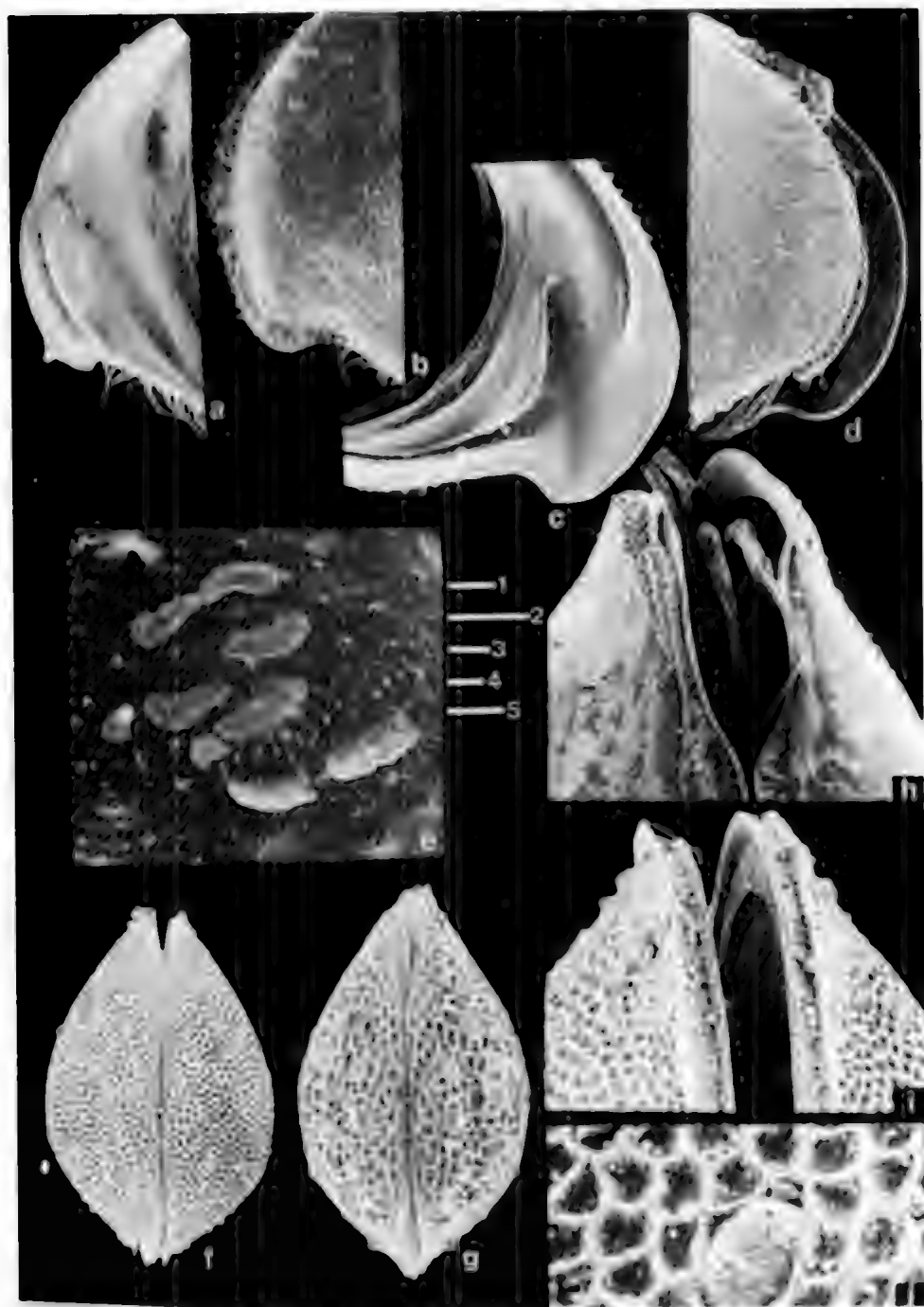


Fig. 4. *Binnelongia australis* (Brady, 1886) a RV internal, detail anterior of Fig. 3d. b LV external, detail anterior of Fig. 3e. c LV internal, detail anterior of Fig. 3a. d C showing RV, detail anterior of Fig. 3i. e LV internal, detail central muscle scar area of Fig. 3g. f C dorsal, enlargement of Fig. 5l. h C ventral, detail anterior of Fig. 5k. i C dorsal, enlargement of Fig. 5o. j C ventral, detail anterior of Fig. 3p. k C dorsal, detail of Fig. 4f. l C ventral, detail of Fig. 4i. a-e: Creek pool flowing across the road, 2 km N of Leonora, W.A. f-j: Roadside pool, 5 km S of Cunderdin, W.A. Scale: 1—100 μ for a-d, h; 2—50 μ for e; 3—100 μ for f; 4—50 μ for g; 5—20 μ for i.



Fig. 5. *Bennelongia australis* (Brady, 1886) a RV internal, female. b LV internal, female. c LV external, female. d RV external, female. e C dorsal, female. f C showing RV, female. g RV internal, juvenile. h LV internal, juvenile. i LV external, juvenile. j RV external, juvenile. k C ventral, female. l C dorsal, juvenile. m C dorsal, juvenile. n C dorsal, juvenile. o C ventral, juvenile. p C ventral, detail posterior of k. q RV internal, detail anterior of a. r LV internal, detail anterior of b. s RV internal, detail posterior of a. a-s: Roadside pool, 5 km S of Cunderdin, W.A. Scale: 1—250 μ for a-o; 2—100 μ for p-s.



Fig. 6. *Bennelongia australis* (Brady, 1886) a antennula, b mandible—palp, c maxillula—palp and lobes, d antenna, e rake-like organ, f hemipenis, g thoracopoda I, h maxilla, male, i maxilla—endopodite, male, j hemipenis, k thoracopoda II, l maxilla—endopodite, female, m furcal attachment, n furca. a-b, d-k, m-n: adult male—creek pool flowing across the road, 2 km N of Leonora, W.A. c, l: adult female. Scale: 200 μ .

Rake-like organ: (Fig. 6c) Five teeth plus another bifid one on inside of each rake.

Maxillular: (Fig. 6c) Length/width ratio of palp segments: 4/1, 4/1; 3rd lobe with two smooth Zahnborsten and tufted thick seta at end of 3rd lobe near Zahnborsten. About 17 plumose Strahlen on epipod plate.

Maxilla: Sexually dimorphic: in female (Fig. 6l) three unequal plumose setae at tip of endopod; in male (Figs 6h,i) grasping palps unequal, broadest one on right side—for chaetotaxy see Fig. 6h.

Thoracopoda I: (Fig. 6g) Geniculate distal part of 1st segment with two setae, proximal one being almost twice as long as other. Penultimate segment weakly divided. Inner distal seta of 2nd segment shorter than 0.5 length of 3rd segment and shorter than distal outer seta of terminal segment. Inner distal end of penultimate segment with two unequal setae. Inner distal seta on the 4th segment is about 0.33 of length of distal claw.

Thoracopoda II: (Fig. 6k) Distal setae unequal; large one more than twice length of other which is hook-shaped. Broad pincers present distally.

Hemipenis: (Figs. 6f,j) Lateral lobe broad with inner distal end pointed and curved inward. Copulatory sheath broadly triangular in shape with round inner distal end reaching almost curved tip of lateral lobe. Outermost point of sheath forms hump and corresponds to mid-length of inner side of sheath.

Zenker organ: With 33 rosettes.

Furca: (Fig. 6n) Claws narrow, long and unequal and posterior seta longest of the two.

Furcal attachment: (Fig. 6m) Bifurcate at distal end; median branch thickest and other two branches arched inwards.

Eye: Dark brown with two lateral silver lenses.

Colour of shell: Green to pale green.

Size.

lectotype: adult left valve

L	ff
LV 1980 μ	1200 μ

adult male

L	ff	L	ff
LV 1860 μ	1060 μ	RV 1740 μ	1100 μ

adult female

L	ff	L	ff
LV 2220 μ	1300 μ	RV 2060 μ	1220 μ

Remarks: Examination of the type specimens of *Chlamydotheca australis* Brady, 1886 in the

British Museum necessitates the following clarification. One adult left valve (L. 1980 μ , H 1200 μ), designed here as the lectotype, is the valve probably illustrated by Brady (1886) on Plate IX.7. The tip of the beak-like feature of this left valve is broken off. In the same slide, there is another left valve which probably belongs to a *Heterocypris* sp. It is likely that this valve is the one thought by Brady (1886) to be the right valve of *C. australis* and illustrated by him on Plate IX.8. It definitely lacks the peripheral posteroventral tubercles and the broad inner lamella anteriorly so typical of all *Bennelongia* species and the anteroventral flange of *B. australis* specimens. This would explain the incorrect description of the right valve of this species provided by Brady (1886, p. 91). Examination of one carapace of *B. australis* from a slide bearing Brady's handwriting in Sars' collection in the Oslo Museum further confirms Brady's misidentification.

Finally, in the same slide from the British Museum, there are two partly broken carapaces of smaller *Bennelongia* species (length 1360 μ , height 800 μ) with some dried soft parts inside. Their specific identification remains uncertain although it is thought they belong to *B. baranzaroo*.

In 1894, Sars synonymized *C. australis* Brady, 1886 with *Cypris bennelong* King, 1855 maintaining that Brady's specimens were the same as those of King, and by stating that the latter author had described the species from juvenile specimens. This was repeated by Sars (1896) and Hentz (1923). Sars' suggestion cannot be accepted because King (1855) stated on page 63 that *C. bennelong* has 'equal valves'. This is not the case for adult *Bennelongia* species. Sars' (1894) argument of King's specimens being juveniles cannot be accepted here either since juveniles of *Bennelongia* (which have symmetrical valves) are either deeply punctated all over or are strongly tuberculated. These features are best seen on specimens described by Sars (1896) as *Cypris lateraria* King, 1855 which are juveniles of *Bennelongia* spp. Either tubercles or pitted shell would have surely been diagnosed by King otherwise.

Sars' specimens described from Australia (Sars 1896) and New Zealand (Sars 1894) as *C. bennelong* are true *Bennelongia* species but do not belong to *B. australis*. Since they cannot be identified as King's species, they are there-

fore renamed here as *B. barangaroo* n.sp.. This species is described below.

Ecology and distribution: *B. australis* was originally collected from Penola, S.A. by Prof. R. Tate. The specimens were empty shells (Brady 1886). This species inhabits mainly temporary pools and, so far, has been found alive only in Western Australia and South Australia. Adult males have been found in a permanent lake in Western Australia, suggesting that the mode of reproduction is parthenogenetic in ephemeral environments.

Localities: W.A.: Roadside pool 2.3 km S of Northcliffe; roadside pool Pfeiffer's Road, 8 km from Mary Peaks; Lake Sadie, east of Wilson Inlet (near Denmark); creek pool flowing across the road 2 km north of Leonora; roadside pool 5 km S of Cunderdin; roadside pool on eastern side of road between Quairading and Corrigin (25 km northwest of Corrigin); Lake Biddy, S.A.: Roadside pool, 3 km east of Rocky River, Kangaroo Island.

Water was fresh except in the last two sites in Western Australia where salinity was 4.4 and 3.5‰ respectively.

***Bennelongia barangaroo* n.sp.**

FIGS 7-8, 9 a-q

1894 *Cypris bennelong* King: Sars, p. 24.

1896 *Cypris bennelong* King: Sars, p. 49.

1896 *Cypris lateraria* King: Sars, p. 53.

1923 *Cypris bennelong* King: Henry, p. 275.

Diagnosis: Area just behind beak-like feature of left valve slightly concave; outline of hemipenis as in Fig. 8j.

Description: *Carapace.* (External) Adult: circular to oval carapace smooth or covered with faint pustules and pilose. Ventrums flattened. Valves asymmetrical: left valve larger, especially anteriorly with largest overlap ventrally; anteroventral region of left valve slightly concave to form beak-like feature whereas right valve broadly rounded and with an elongated and narrow beak-like serrated flange anteroventrally. Simple type normal pore canals.

Juvenile: More elongated in lateral view, with symmetrical, pitted or tuberculated valves. (Internal) Adult: Inner lamella twice as broad anteriorly in both valves, selvage peripheral ventrally, away from outer margin posteriorly and especially anteriorly; inner list forming lip-like flap far away from edge of shell anteroventrally which is preceded by a deep, narrow groove. A ridge follows curvature of inner margin anteriorly but fades opposite tongue-

like flap. Few small tubercles are visible on this ridge above concave depression of shell. Outer list often broad posteroventrally. In right valve, selvage peripheral and sharp posteriorly, broad anteroventrally and faint anterodorsally. In many specimens, edge of shell near flange distorted to form an obvious concavity which is paralleled by a depression. A row of tubercles along periphery of shell posteroventrally. Outer list also broader posteroventrally and usually pitted externally near edge of shell; this is best seen in ventral area. *Juvenile:* In both valves, inner lamella of almost equal width all around and selvage, which follows the curvature of the shell, prominent.

Anatomy: Only the features of the anatomy which differ significantly from *B. australis* and other *Bennelongia* species are mentioned. For other details refer to Fig. 8.

Antennula: Natatory setae slightly longer than all segments together.

Maxilla: Male grasping palps (Figs 8g,h) of different shape than *B. australis*: left palp shorter and broader and right one with outer edge forming 90°.

Thoracopoda I: (Figs 8d,e) Inner distal seta of second segment at least as long as half of 3rd segment; longest inner seta at mid-length of 3rd segment (where it is weakly divided) at least as long as 2nd half of 3rd and 4th segments together. Inner distal seta on 4th segment 1/2:3 of length of distal claw.

Colour of shell: Green.

Size:

holotype adult male

	L	H		L	H
LV	1120µ	700µ	RV	1100µ	660µ

paratype adult female

	L	H		L	H
LV	1160µ	700µ	RV	1110µ	680µ

Newmann's Rocks adult female

	L	H		L	H
LV	1390µ	780µ	RV	1320µ	770µ

Derivation of name: From the aboriginal name of Bennelong's wife Barangaroo.

Type locality: Lake Buchanan, Qld (21°35'S, 145°52'E).

Ecology and distribution: *B. barangaroo* is a common inhabitant of temporary pools and usually is only represented by parthenogenetic females. On one occasion, in Lake Buchanan, both sexes were found. There salinity was

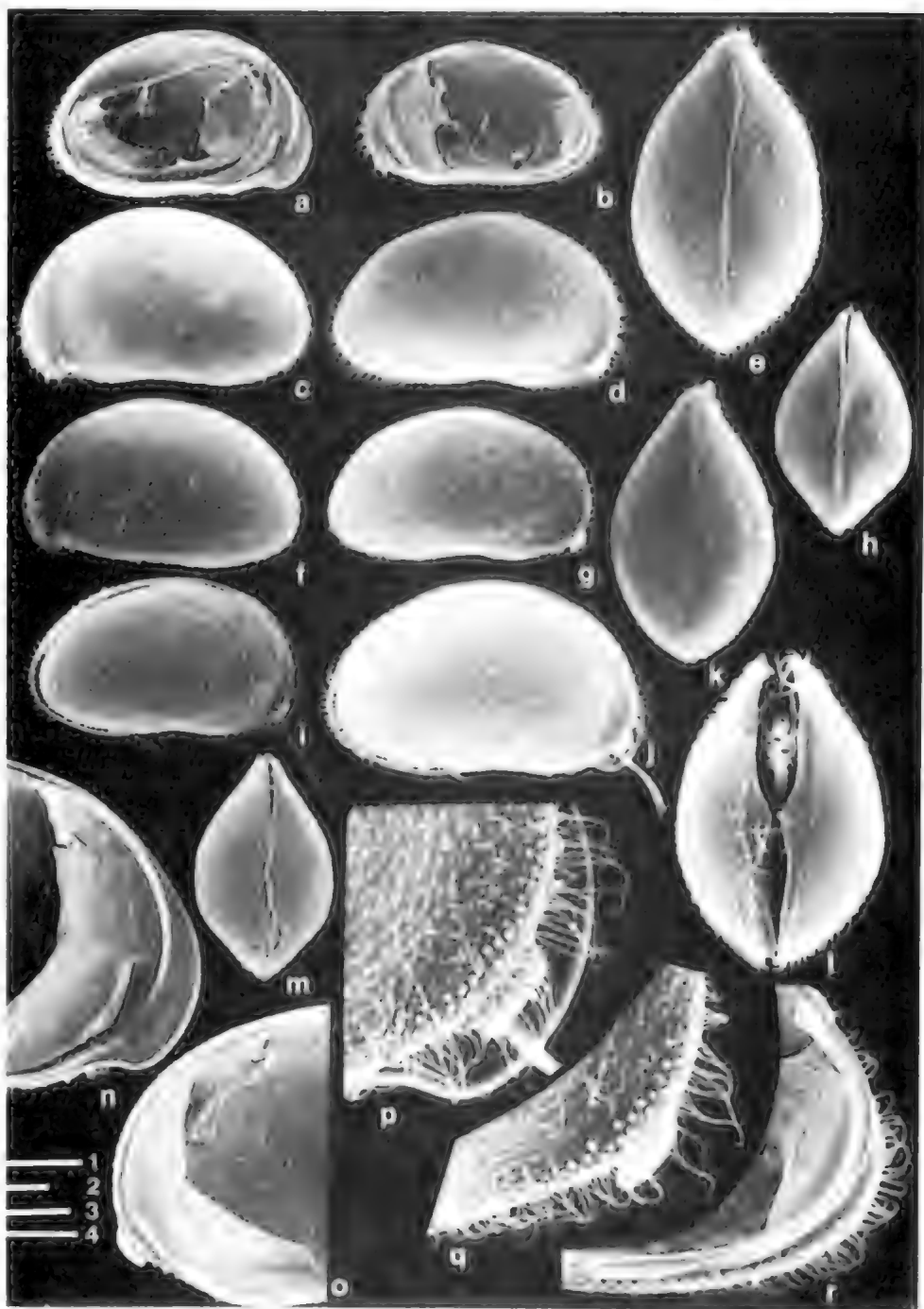


Fig. 7. *Bennelongia barangaroo*, n.sp. a LV internal, holotype male, b RV internal, holotype male. c LV external, paratype female. d RV external, paratype female. e C dorsal, paratype female. f LV external, paratype male. g RV external, paratype male. h C dorsal, juvenile. i C showing RV, paratype male. j C showing RV, paratype female. k C dorsal, paratype male. l C ventral, paratype female. m C ventral, juvenile. n LV internal, detail anterior of paratype female. o RV internal, detail anterior of paratype female. p C showing RV, detail anterior of j. q RV external, detail anterior of d. r RV internal, detail posterior of b. Scale: 1—250 μ for a-m; 2—100 μ for n-o; 50 μ for q; 3—50 μ for p; 4—100 μ for r.

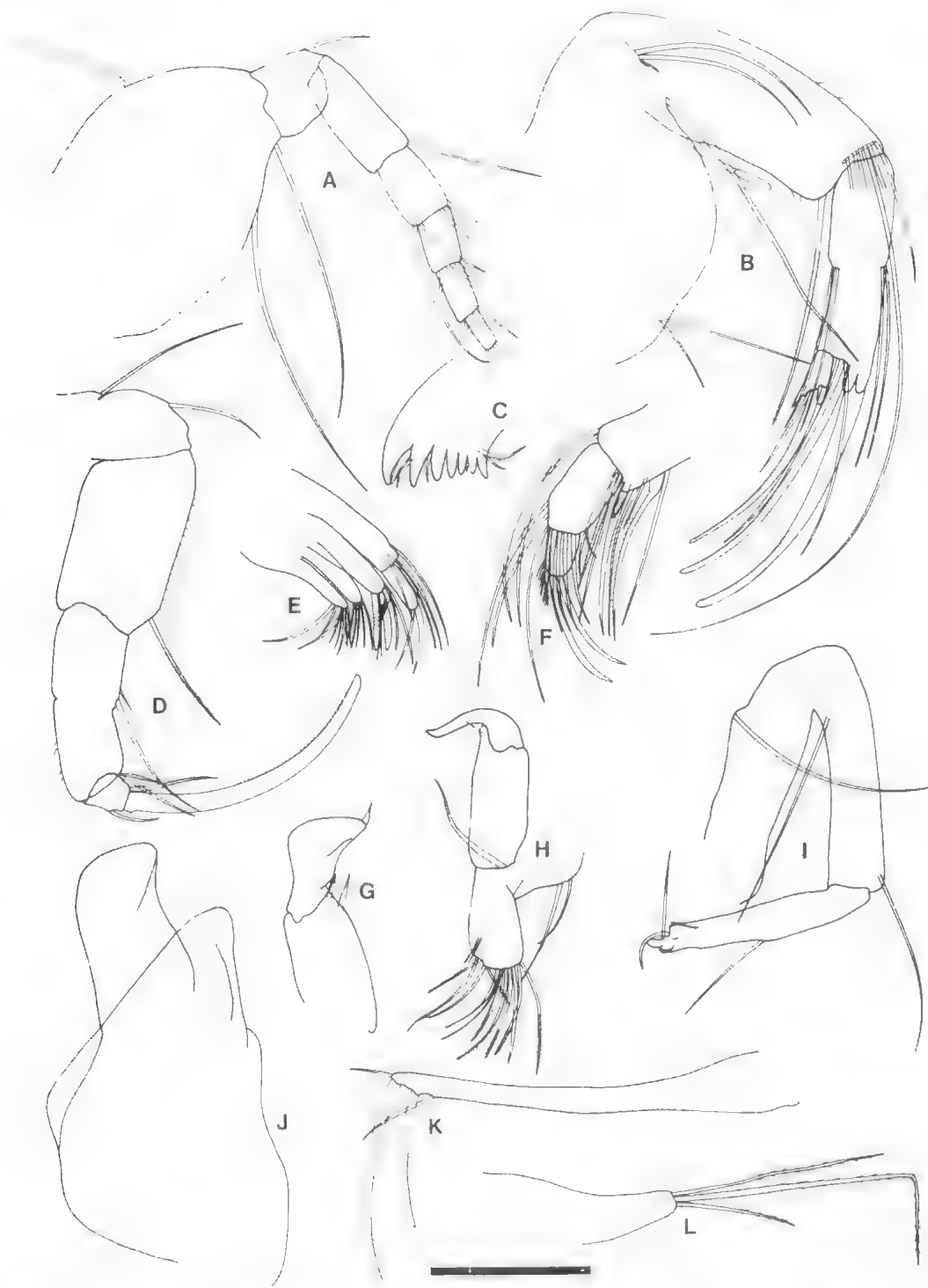


Fig. 8. *Bennelongia barangaroo*, n.sp. a antennula, b antenna, c mandible—coxale, d thoracopoda I, e maxillula—palp and lobes, f mandible—palp, g maxilla—endopodite, male, h maxilla; male, i thoracopoda II, j hemipenis, k furca, l maxilla—endopodite, female, a-b, d-k: holotype adult male; c l: paratype adult female. Scale: 100 μ .

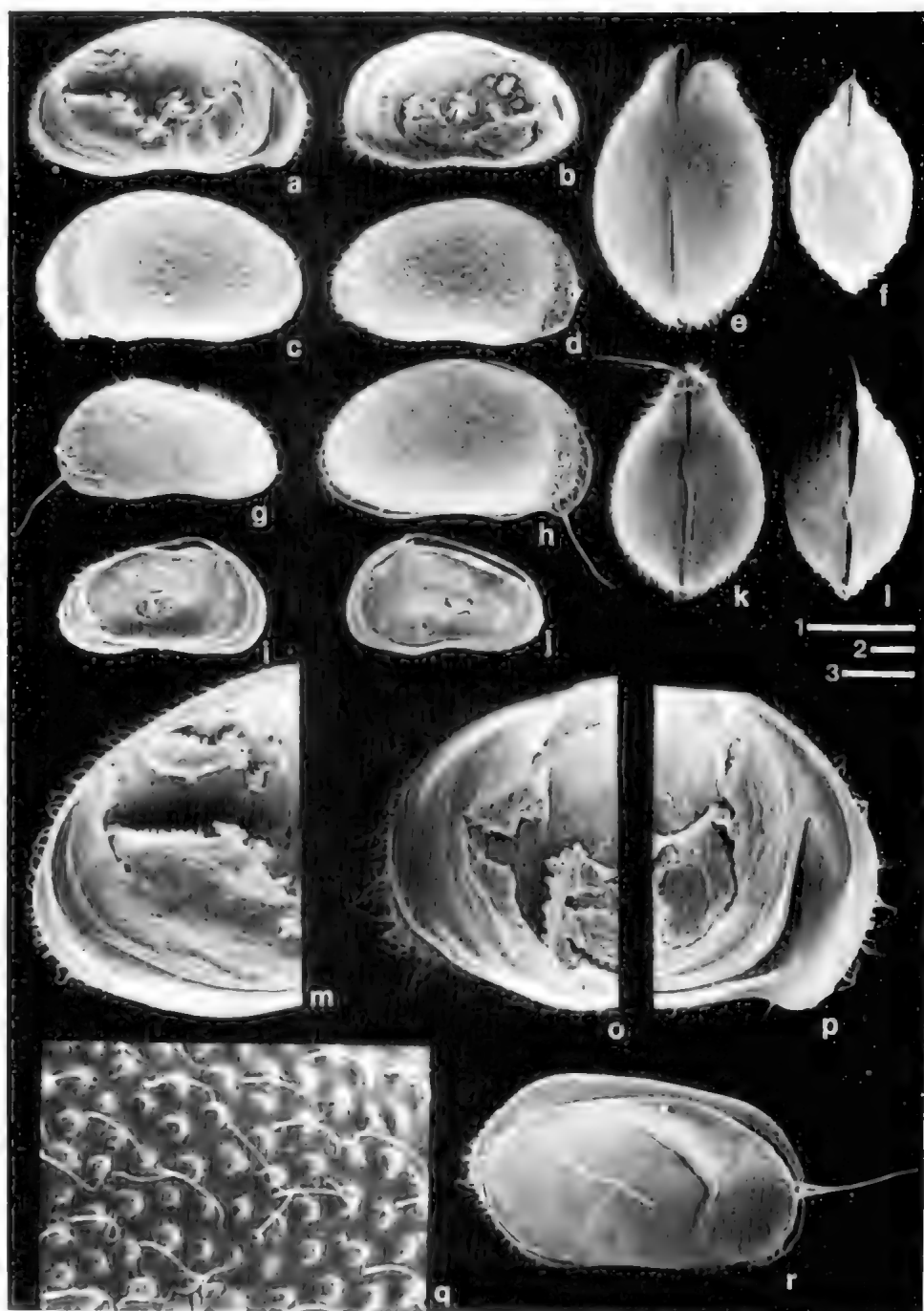


Fig. 9. *Bennelongia barangaroo* n.sp. a LV internal, female. b RV internal, female. c LV external, female. d RV external, female. e C dorsal, female. f C dorsal, juvenile. g C showing LV, juvenile. h C showing RV, female. i LV internal juvenile. j RV internal juvenile. k C ventral, female. l C ventral, juvenile. m LV internal, posterior detail of a. o RV internal, anterior detail of b. p LV internal, anterior detail of a. q C dorsal, detail of e. a-q: elongated pool in creek bed, about 25 km N of Cue, W.A. *Bennelongia* sp. r C showing RV. Cauckingburra Swamp, at Lake Buchanan, via Charters Towers, Qld. Scale: 1—500 μ for a-k; 2—100 μ for m-p; —20 μ for q; 3—500 μ for r.

4.1%. In other localities listed below, water was known to be fresh.

Live specimens with tuberculated symmetrical valves collected in a farm dam at Frome Downs near Lake Frome, S.A., were examined in the laboratory. They resembled specimens illustrated by Sars (1896a) on Plate VII: Fig. 3 and labelled by him as *Cypris lateraria* King, 1855. After a few days, these specimens, which had traces of ovaries inside the valves, were seen to molt into *B. barangaroo* with its typical asymmetrical valves. Eggs of the latter developed into small highly ornamented ostracods like *C. lateraria*. This phenomenon requires the two taxa to be synonymized.

Localities: W.A.: granite pool, Newmann's Rocks, 140 km E of Norseman; roadside ditch 37 km W of Esperance (road to Ravens-thorpe) and 3.5 km east of Dalyup River; small roadside pool about 18 km northeast of Menzies; elongated pool in bed of Cookarow Creek, about 5 km W of Wiluna; pool in creek bed about 25 km N of Cue; small farm dam on eastern side of road 9 km S of Cunderdin on the way to Quairading, S.A.; Farm dam at Frome Downs, near Lake Frome, Qld; Creek, 22 km E of Richmond; roadside pool at Miranda; Lake Galilee, near Aramac; Lake Dunn, south of Lake Galilee, N.S.W.: Specimens raised by Sars from sample of dried mud collected in waterholes by Mr Whitelegge in Bourke Street, Sydney (Sars 1896). New Zealand: Specimens raised from dried mud sample collected near Kaitia in the North Island. Chapman (1963) stated that this species had not been found in New Zealand since Sars' (1894) description and no further localities are provided in Chapman & Lewis (1976).

Remarks: *B. barangaroo* is closely allied to *B. australis* but the species can be separated on the basis of size (*B. australis* is much larger), on the outline of the hemipenis and the chaetotaxy of the thoracopoda I.

The specimens of *B. barangaroo* described here are identical in morphology to Sars' specimens from Bourke Street, Sydney and from New Zealand. It is assumed here that the specimens reported as *Cypris lateraria* by Sars (1896) from the Sydney site are juveniles of *B. barangaroo*.

The shape and width of the anteroventral flange on the right valve of *B. barangaroo* can vary extensively: in the specimens from Lake Buchanan, the edge of the flange is serrated (Figs 7p,q).

Bennelongia nimata n.sp.

FIGS 10-11

Diagnosis: Oval to subrectangular, pustulose carapace with posterior slightly pointed and ending with one or two spines. Hump-like thickening of shell anterodorsally. Posterior seta of furca about 0.7 of length of posterior claw and lateral outline of hemipenis as in Fig. 11g.

Description: Carapace. (External) Adult: Oval to subrectangular-shaped with posterior slightly pointed and ending with one or two spines. In dorsal view, egg-shaped with anterior end narrow and more pointed than posterior. Valves obviously asymmetrical in anteroventral area: there, left valve formed like pointed beak whereas in right valve, it is broadly rounded and there is a small beak-shaped serrated flange. Posterior to flange, edge of right valve slightly concave. Tip of beak does not reach horizontal plane formed by ventral area. Greatest height at about 0.33 from anterior. Shell pilose, pseudopunctated and pustulose nearly all over. Along edge of left valve, especially, pustules more concentrated and some are pointed, especially anteriorly.

Juvenile: Pseudopunctate, subtriangular shell with many pointed tubercles scattered all over but with greater concentration anteriorly and posteriorly. Valves symmetrical. In dorsal view, oval-shaped with both ends pointed.

(Internal) Adult: Inner lamella broadest anteriorly in both valves. In left valve, selvage narrow and peripheral; inner list forming lip-like flap anteroventrally. This flap fades in anterodorsal region. In front of flap in ventral area, a deep narrow groove. Between outer margin and just behind beak ventrally, is a ridge which is tuberculate in some specimens. In anterior area, in front of hinge area, is a deep groove running parallel to curvature of shell which is placed near outer margin. This groove absent in beak-like area. In right valve, selvage narrow and runs parallel to curvature of shell except at mid-height anteriorly where it is not visible. Anteriorly, in region where serrated flange present, a small ridge runs parallel to, and between, selvage and inner margin.

Juvenile: Inner lamellae equal in both valves and of same width all along. Selvage broad and peripheral.

Anatomy: Same remarks as for *B. barangaroo*. For details of anatomy, refer to Fig. 11.

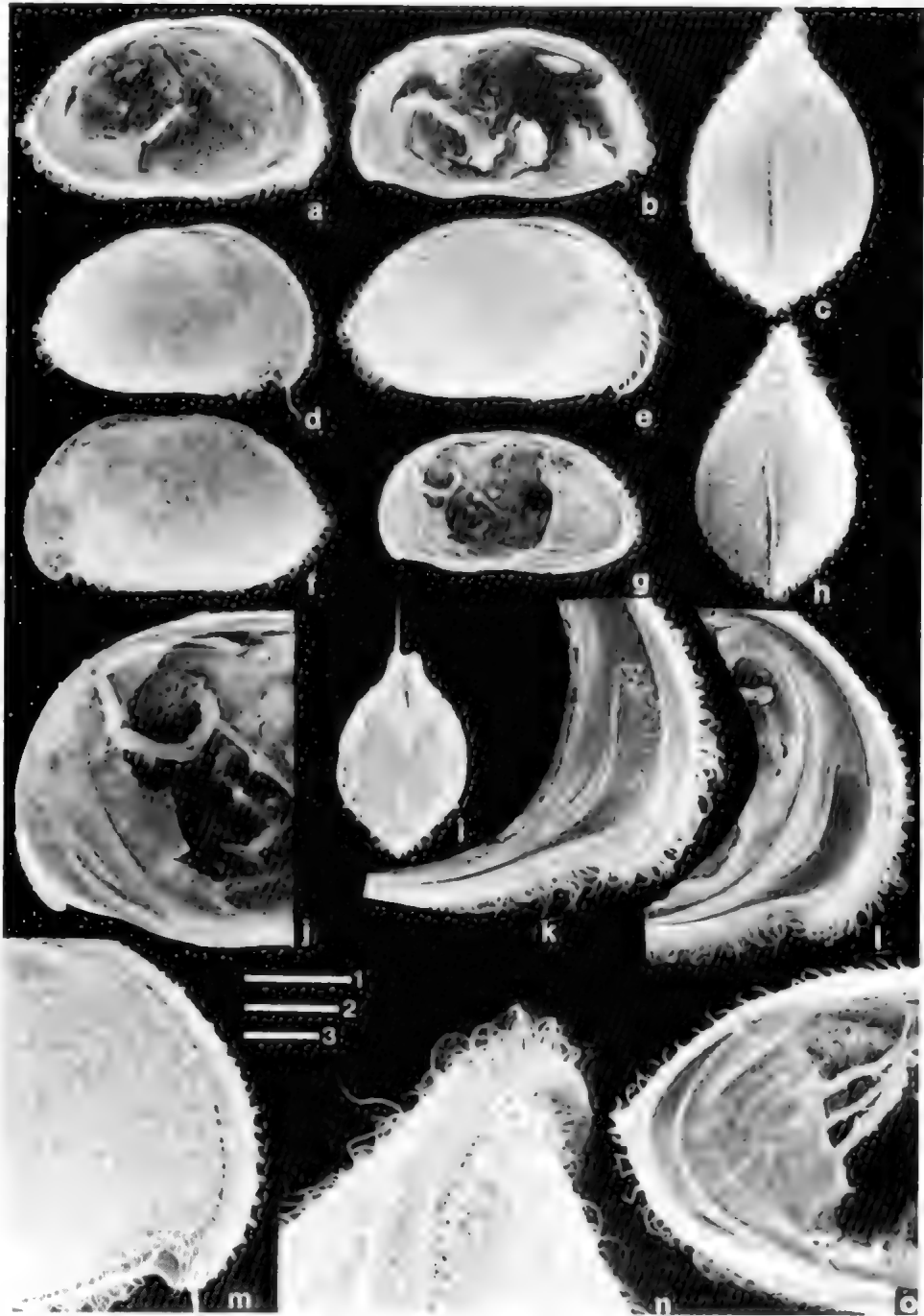


Fig. 10. *Bennelongia nimala* n.sp. a LV internal, female paratype. b RV internal, female paratype. c C dorsal, female paratype. d C showing RV, male. e C showing RV, female paratype. f C showing LV, female paratype. g RV internal, male holotype. h C ventral, male paratype. i C dorsal, juvenile. j RV internal, anterior detail of g. k LV internal, anterior detail of a. l LV internal, anterior detail of d. m C showing RV, anterior detail of d. n C dorsal, anterior detail of c. o LV internal, posterior detail of male paratype. a-c, e-h, j-l, n-o: Georgetown Lagoon, near Jabiru, N.T. (type locality). d, i, m: Buffalo Billabong, near Jabiru, N.T. Scale: 1—500 μ for a-i; 2—200 μ for j-m, o; 3—100 μ for n.

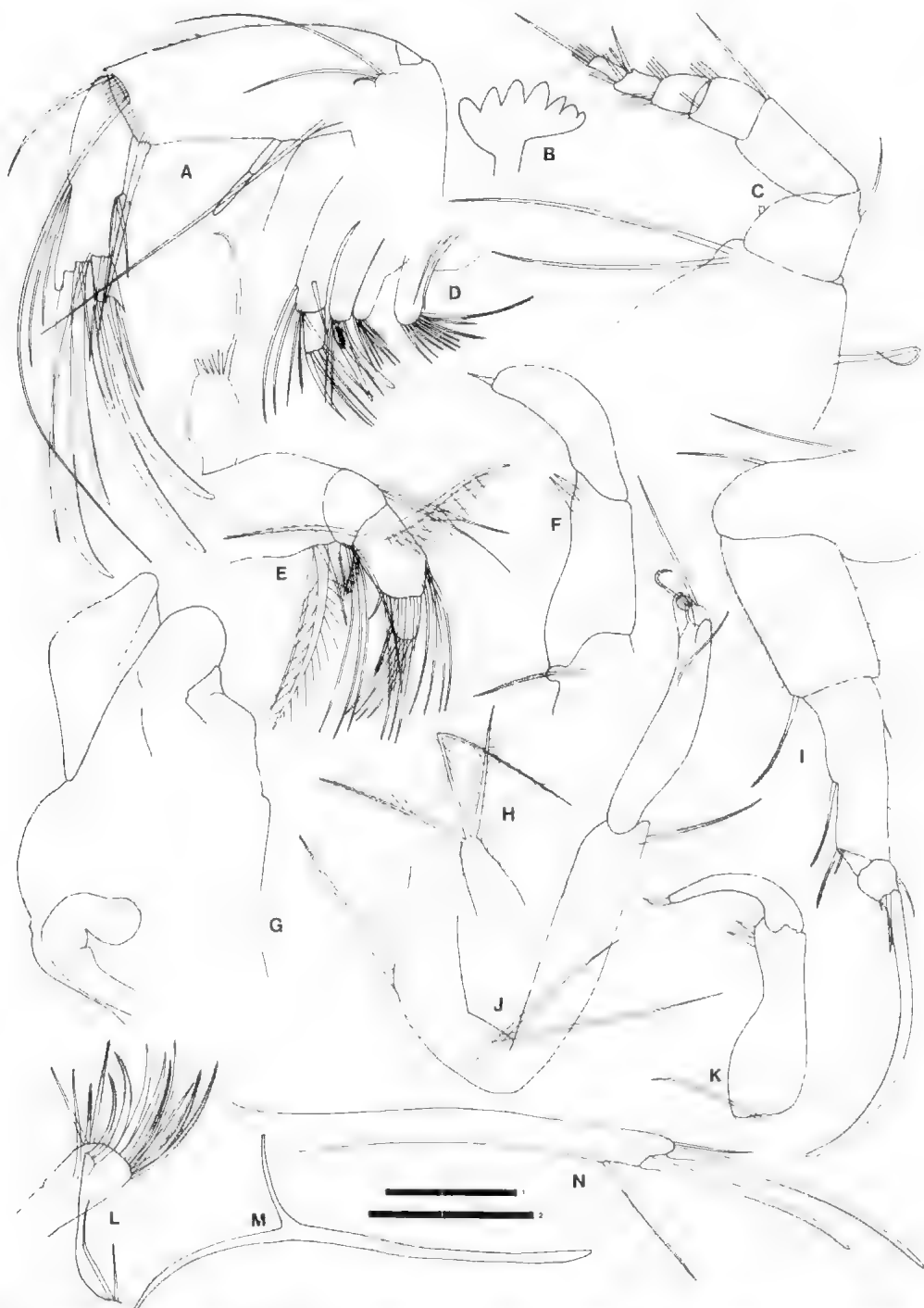


Fig. 11. *Bennelongia nimala* n.sp. a antenna, b rake-like organ, c antennula, d maxillula—palp and lobes, e mandible—palp, f maxilla—endopodite, male, g hemipenis, h maxilla—endopodite, male, i thoracopoda I, j thoracopoda II, k maxilla—endopodite, male, l maxilla—protopodite, female, m furcal attachment, n furca. a-c, e-g, i, k-m: holotype adult male; d, h, j, n: paratype adult male. Scale: 1—100 μ for a, c-n; 2—50 μ for b.

Antennula: (Fig. 11c) Natatory setae as long as all segments together.

Maxilla: Male palps asymmetrical (Figs 11f,k) with right one broader and less arched. Two external setae on female palp (Fig. 11h) of equal length and plumose.

Thoracopoda I: (Fig. 11i) Inner distal seta of 2nd segment almost reaches weakly divided area in middle of 3rd segment where another seta of similar length occurs. Inner distal seta of 4th segment 1/5.6 of length of distal claw. Hemipenis: (Fig. 11g) Lateral lobe broad: greatest length equals its greatest width. Near base of lateral lobe on inner side, copulatory sheath in form of circular lump.

Zenker organ: Funnel-shaped at both ends, with 30 rosettes.

Furca: (Fig. 11n) Posterior seta long, approximately 0.7 length of posterior claw.

Colour of shell: Green to dark green with broad transversal white stripes best seen in dorsal view.

Size:

holotype adult male

L	H	L	H
LV 1500 μ	840 μ	RV 1340 μ	760 μ

paratype adult female

L	H	L	H
LV 1640 μ	960 μ	RV 1540 μ	860 μ

Type locality: Georgetown Lagoon, Jabiru, Northern Territory.

Derivation of name: The word *nimala* in aboriginal language of the Northern Territory means lagoon, for the typical habitat of this species.

Ecology and distribution: *B. nimala* is a freshwater species found in lagoons near Jabiru, east of Darwin, N.T.; Jabiluka Billabong, Buffalo Billabong and Mudginberri Lagoon. Both sexes were always found in the collections.

***Bennelongia pinpi* n.sp.**

FIGS 12-13

Diagnosis: Anteroventral area of left valve strongly beak-shaped extending below horizontal plane of flat ventral area. In dorsal view, carapace almost circular, with both ends broadly pointed. Outline of hemipenis as in Fig. 13e.

Description: Carapace. (External) Adult: triangular to semicircular with flat ventral area; greatest height at about middle. Anteroventral area of both valves beak-like but more pronounced in left valve. Surface of shell smooth to pseudopunctate and barren of hairs except

in mouth region. In dorsal view, carapace almost circular with anterior and posterior ends broadly pointed. At about 0.17 from anterior, shell pinched, being more noticeable in posteroventral area. Valves strongly asymmetrical anteroventrally where left valve larger, elsewhere left valve slightly overlapping right valve.

Juvenile: Subtriangular with ventrum almost flat and greatest height at about 0.4 from anterior. In dorsal view, carapace oval to almost circular with both ends pointed. Largest juveniles with pseudopunctated shell and few tubercles. In very small juveniles, shell pitted and thinly reticulated and with some sieve plates. Most tubercles are cone-shaped and a hair protrudes from each of them. Valves almost symmetrical with left slightly larger.

(Internal) Adult: Inner lamella much broader anteriorly in both valves. In left valve, inner list forms broad lip anteroventrally and is absent anterodorsally. Selvage narrow ventrally and distant from outer margin and broader posteroventrally where it is placed in middle of inner lamella. Above concavity behind beak-like form in anterior of shell, there are a few tubercles between outer margin and lip-like inner list. Depression in front of lip-like inner list and another near outer margin antero-dorsally. In right valve, selvage narrow and peripheral. A broad tongue-like flange antero-ventrally in some valves which is enclosed by broader beak-like left valve when carapace closed. An outer list runs parallel to curvature of right valve and bordered by small tubercles ventrally except in mouth region.

Juveniles: Inner lamellae twice as broad anteriorly and with broad and prominent selvage following curvature of shell. Outer list runs parallel to curvature of both valves and bordered inside by faint tubercles in some juveniles.

Anatomy: As for other species. For details of the anatomy, see Fig. 13.

Antennula: (Fig. 13b) Natatory setae almost as long as all the segments together.

Maxillula: Male palps (Figs 13i,j) asymmetrical with right one broader although both are similarly arched.

Thoracopoda I: (Fig. 13g) Inner distal seta on 2nd segment almost reaches level of weak division of 3rd segment. There, inner distal seta long, extending past 4th segment. Length

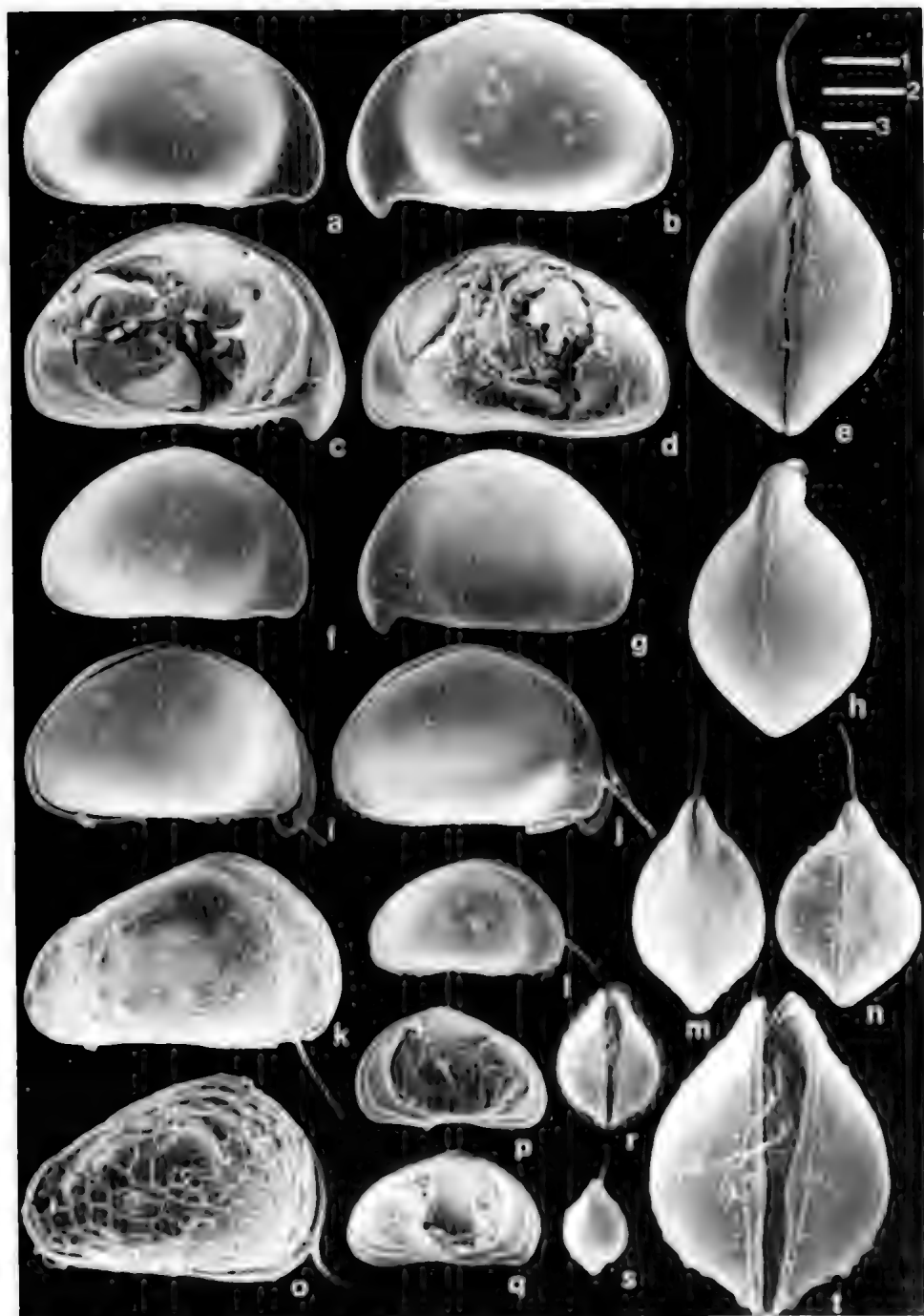


Fig. 12. *Bennelongia pinpi*, n.sp. a RV external, female paratype. b LV external, female paratype. c LV internal, female paratype. d RV internal, female paratype. e C ventral, female paratype. f RV external, male holotype. g LV external, male holotype. h C dorsal, male paratype. i C showing RV, male paratype. j C showing RV, female paratype. k C showing RV, juvenile. l C showing RV, juvenile. m C dorsal, juvenile. n C ventral, juvenile. o C showing RV, juvenile. p RV internal, juvenile. q LV internal, juvenile. r C ventral, juvenile. s C dorsal, juvenile. t C ventral, enlargement of r. Scale: 1—500 μ for a-p, l-n, p-s; 2—200 μ for k; 3—150 μ for o.



Fig. 13. *Bennelongia pinpi*, n.sp. a maxillula—pulp and lobes, b antennula, c antenna, d mandible—palp, e hemipenis, f maxilla—endopodite, female, g thoracopoda I, h thoracopoda II, i maxilla, male, j maxilla—endopodite, male, k furca, l furcal attachment. a-c, e, g-k: holotype adult male; d, f, l: paratype adult female. Scale: 200 μ .

ratio of distal seta of 4th segment and distal claw is 1/3.5.

Hemipenis: (Fig. 13c) Outer lobe broad and digitate and, near its base on inner side, copulatory sheath forms broad trapezoid-shaped extension.

Zenker organ: With 42 rosettes.

Furca: (Fig. 13k) Setae almost equal-posterior one longer and about 0.5 length of posterior claw.

Colour of shell: Light green.

Sizes:

holotype adult male

I	II	L	H
IV 2480 μ	1600 μ	RV 2340 μ	1420 μ

paratype adult female

I	H	L	H
LV 2580 μ	1640 μ	RV 2440 μ	1520 μ

Type locality: Pine Tree Creek Lagoon, N of Hughenden, and exactly 16 km S of Louisa Lake on road to Hughenden, Qld (20°00'30" S, 144°16'44" E).

Derivation of name: The aboriginal word *pinpi* in Queensland meaning parrot is chosen for the anteroventral area of the shell which resembles the beak of a parrot.

Ecology and distribution: This freshwater species is known from three other localities in Queensland: Agnes Lake, Salt Lake (fresh) and Louisa Lake, all three N of Hughenden.

SUBFAMILY: EUCYPRIDINAE Bronstein, 1947

Australocypris De Deckker, 1974

Type species: *Australocypris robusta* De Deckker, 1974.

Remarks: The following species are discussed in the present work and can be distinguished on the outline of the hemipenis: *A. dispar* n.sp., *A. insularis* (= *A. hypersalina*), *A. rectangularis* and *A. robusta*. All *Australocypris* species are halobiont and planktic but can also crawl on lake floors. Rarely do two species occur together in one lake.

Australocypris dispar n.sp.

FIGS 14, 15 a-i

Diagnosis: Lateral lobe of hemipenis digitate and broad at base; long distal seta on 4th segment of thoracopoda I.

Description: **Carapace.** (External) Pseudopunctate, subrectangular carapace with an-

terior end broadly rounded, dorsum slightly inclined and posterior steeply inclined. Ventrums strongly concave past mid-length from the anterior. Greatest height at about 0.4 in female and 0.33 in male. In dorsal view, carapace elongated, length more than twice width, and both extremities slightly pointed. Left valve slightly larger in female and ventral overlap minimal. Both valves extend over one another in anterodorsal area just before hinge. Simple normal pore canals.

(Internal) Inner lamella narrow in both valves and selvage faint and between edge of valve and selvage which is prominent in that area. Radial pore canals numerous and straight. Central muscle field consisting of five adductor scars and two large mandibular ones in front and below.

Anatomy: **Antennula:** (Fig. 14c) Length/width ratio of last six segments: 2/3, 2/1, 1/1, 5/3.5, 2/1.4, 4/3. Small wart-like "sensory" organ on side of 2nd segment. **Nata-tory setae** as long as last six segments together. **Antenna:** (Fig. 14a) Massive and sexually dimorphic: four claws in male and three in female; smallest one in male attached to last segment and with long comb-like teeth. **Nata-tory setae** almost reaching tip of claws.

Mandible: Mandibular coxale (Fig. 14h) with seven teeth, the last one longer, narrower than penultimate and, at base, three setae occur, two of which are pilose. **Endopod** (Fig. 14d) with α bristle short, narrow and barren; β bristle stout and finely pilose; γ bristle twice as long as others and pilose in distal half. Distal segment of endopod 0.33 of length of penultimate segment.

Rake-like organ: Seven short and stout teeth plus one inner bifid one on each rake.

Maxillula: (Fig. 14b) Endopod with 23 plumose Strahlens; length/width ratio of palps: 3/1.3, 1.5/1.1 with last segment slightly trapezoidal. Two toothed Zahnborsten on 3rd lobe.

Maxilla: Sexually dimorphic: in male (Figs 14j,k), palps almost symmetrical, strongly curved and narrow; in female (Fig. 14f), palp faintly divided at its extremity and with three short pilose setae, the middle one being twice as long as others.

Thoracopoda I: (Fig. 14e) Penultimate segment weakly divided; distal segment with long inner seta 0.5 length of distal claw. **Thoraco-**

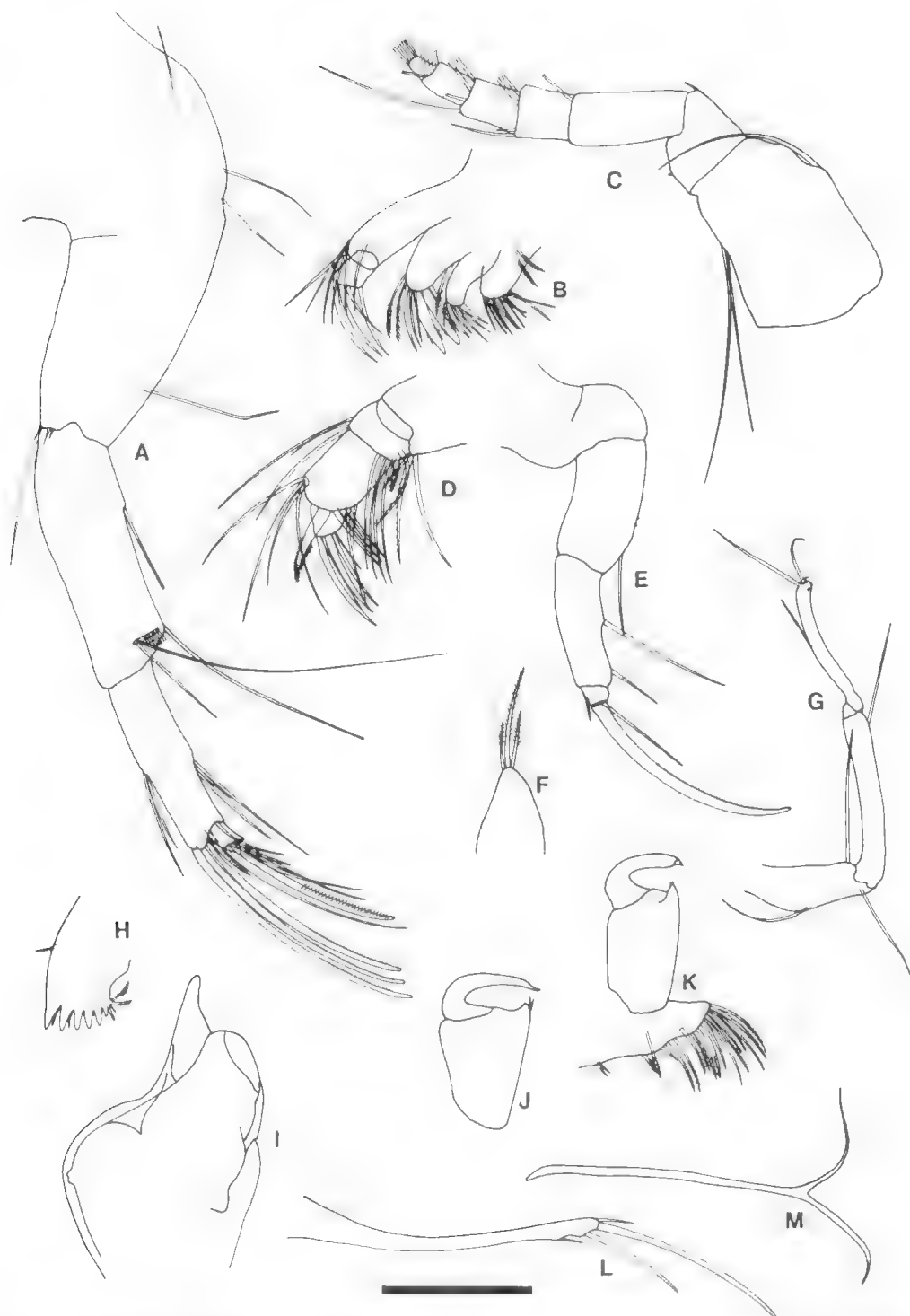


Fig. 14. *Australocypris dispar* n.sp. a antenna, b maxillula—palp and lobes, c antennula, d mandible—palp, e thoracopoda I, f maxilla—endopodite, female. g thoracopoda II, h mandible—coxale, i hemipenis, j maxilla—endopodite, male, k maxilla, male, l furca, m furcal attachment. a, c-e, g-m: holotype adult male; b, f: paratype adult female. Scale: 200 μ .

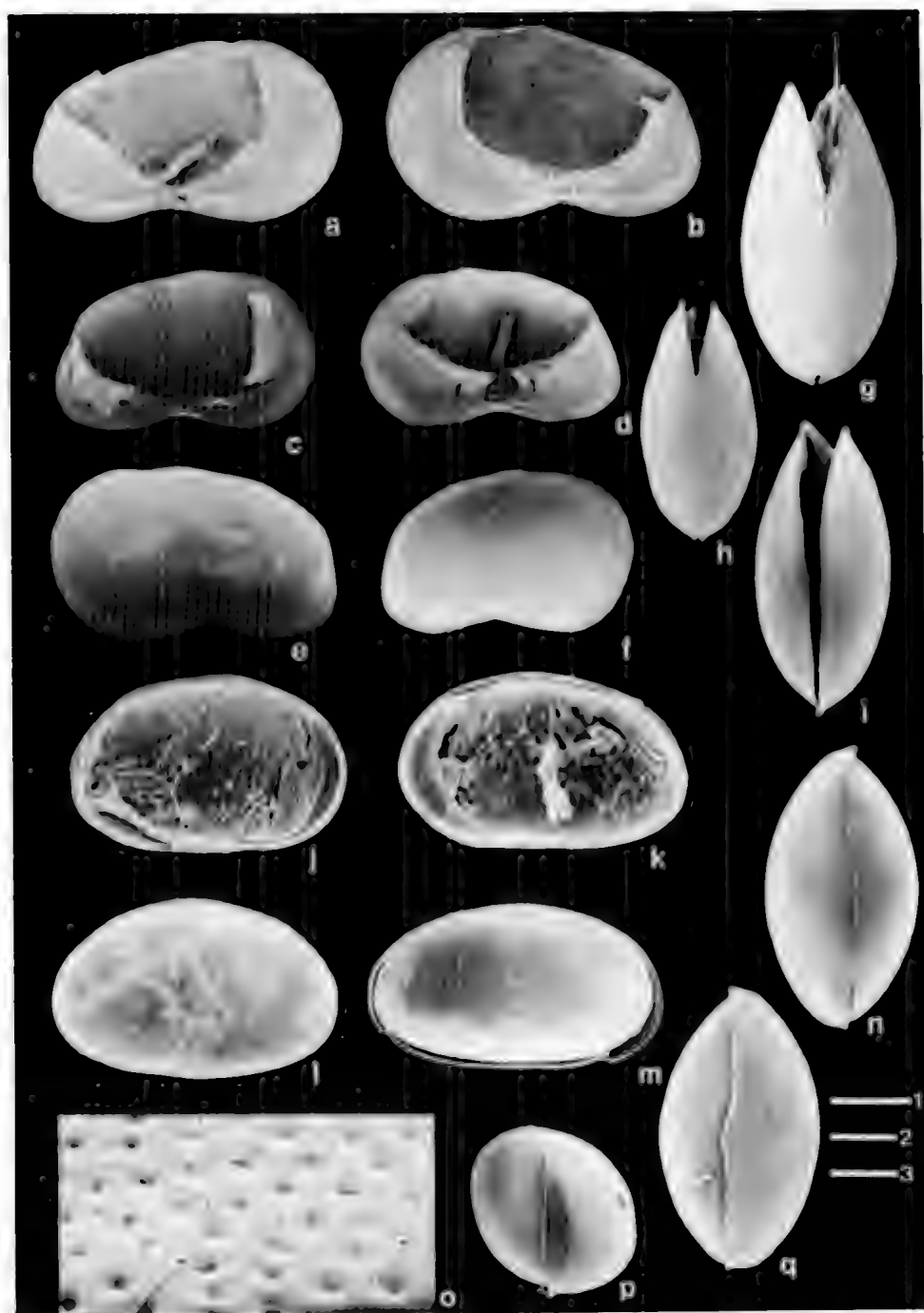


Fig. 15. *Australocypris dispar* n.sp. a LV internal, female paratype. b RV internal, female paratype. c LV internal, male holotype. d RV internal, male holotype. e C showing LV, female paratype. f C showing RV, male paratype. g C dorsal, female paratype. h C dorsal, male paratype. i C ventral, female paratype. *Strandesia phoenix* n.sp. j LV internal, female holotype. k RV internal, female holotype. l C showing LV, female paratype. m C showing RV, female paratype. n C dorsal, female paratype. o C anterior, detail of p. p C anterior, female paratype. q C ventral, female paratype. Scale: 1—1000 μ for a-i; 2—200 μ for j-n, p-q; 3—20 μ for o.

poda II: (Fig. 14g) Elongate and narrow segments distal segment with two terminal setae and two pincers; shortest seta hook-shaped.

Hemipenis: (Fig. 14i) Lateral lobe digitate and slightly curved inwards and broad at its base; copulatory sheath broadly heart-shaped. Zenker organ: Long and narrow with both ends rounded and usually 67 rosettes.

Purca: (Fig. 14j) Unequal claws with anterior one 0.66 longer, and anterior seta slightly longer than posterior one.

Furcal attachment: (Fig. 14m) Proximal part bifurcate; dorsal branch strongly arched and about same length as ventral one which follows curvature of median branch.

Colour of shell: Nacreous brown.

Size:

holotype adult male

L		H	
LV	3600 μ	RV	3600 μ

paratype adult female

L		H	
LV	4100 μ	RV	4000 μ

Type locality: Ephemeral salt lake south of the Coorong Lagoon, S.A. (36°26'45"S, 139°47'32"E) = loc. 5 in De Deckker & Geddes, 1980, collected on 16.X.1978 at 15.5‰ salinity.

Derivation of name: From Latin *dispar* meaning different for the unusual long distal seta on the last segment of the thoracopoda I compared to congeners.

Ecology and distribution: *A. dispar* is a halobiont species which occurs in ephemeral saline lakes in S.A. Near the Coorong Lagoon, its salinity range is 9–52‰, De Deckker & Geddes (1980) provide further details on its distribution there as "*A. n.sp.1*". It is also recorded on the Yorke Peninsula at 6‰ in an ephemeral lake (35°03'11"S, 137°35'50"E) and on the Eyre Peninsula in a swamp south of the road near Lake Horn, northwest of Port Lincoln at 32.4‰.

Remarks: *A. dispar* is characterized by the unusually long seta on the distal segment of the thoracopoda I and the faintly divided end of the female maxillar endopodite palp. These characteristics are unknown in other *Australocypris* species but are found in the halobiont ostracod *Limnocypris luridus* Shornikov, 1961, described from the Kuban Delta in the Caspian Sea region of the USSR. Correspondence with Dr E. Shornikov has led to the conclusion that other features of the chaetotaxy of

many appendages between *A. dispar* and *L. luridus* differ too greatly to justify close relationship between the two species.

Australocypris insularis (Chapman, 1966)

1966 *Eucypris insularis*: Chapman, p. 375.

1974 *Australocypris hypersalina*: De Deckker, p. 101.

1978 *Australocypris hypersalina*: De Deckker, p. 16.

1978 *Australocypris insularis*: De Deckker, p. 17.

Remarks: After examination of many collections of *A. insularis* from Western Australia (from where the species had originally been described), it became clear that *A. insularis* and *A. hypersalina* are conspecific. Both taxa have very similar hemipenes with the characteristic broad and curved lateral lobe and the bulbous inner distal end of the copulatory sheath. This type of lateral outline of the hemipenis is not found in congeners.

The examination of many specimens of *Australocypris* has led to the conclusion that there are slight differences in the morphology of many specimens of *A. insularis* and *A. hypersalina*. Therefore the minor differences of the outline of the hemipenis for the two taxa originally mentioned by De Deckker (1978) are here considered insignificant.

During the revision of all mytilocypridin species (De Deckker 1978), it appeared that *A. insularis* and *A. hypersalina* differed mainly on characters of the shell, but it has since become apparent that the shape of the shell of the *Australocypris* species is also variable in populations taken during different seasons in the same lake. Large specimens collected during winter and early spring months are usually more elongated. For the same reason, the specimens illustrated in De Deckker, 1978, in Figs 18a,b as *A. hypersalina* show the typical winter form of *A. hypersalina* = *A. insularis* not recognized then, as most collections described in that publication had been taken during summer months.

Ecology and distribution: The distribution of *A. insularis* (plus *A. hypersalina*) was dealt with in De Deckker (1977, 1978) and is updated here. The species is commonly found in ephemeral saline lakes near the Coorong Lagoon (see De Deckker & Geddes 1980) where it is found between 5 and 131‰ salinity. It also occurs on the Yorke and Eyre Peninsula in similar ephemeral lakes at the same salinity range. It has also been widely collected

in 15 West Australian salt lakes by Geddes *et al.* (1981) over the range of 2.9–122.6‰.

Australocypris rectangularis De Deckker,
1978

1978 *Australocypris? rectangularis*: De Deckker, p. 17.

1980 *Australocypris rectangularis*: De Deckker & Geddes, p. 691.

Diagnosis: Lateral lobe of hemipenis narrow and hook-shaped; copulatory sheath almost semicircular. Carapace rectangular.

Remarks: The original description of this species was incomplete because a number of appendages had dried out and had been damaged. A number of specimens have since been collected in saline lakes near the Coorong Lagoon by De Deckker & Geddes (1980). They examined the appendages of this species and on morphological grounds referred it with confidence to *Australocypris*.

Ecology and distribution: This species is a true halobiont form which has never been found in salinities below 50‰. Near the Coorong Lagoon, its salinity range is 50–195‰ and there is evidence there that it even hatched above 73‰ and 115‰ in two different localities. On the Yorke and Eyre Peninsulas, *A. rectangularis* occurs in the same range of salinities as in the lakes near the Coorong Lagoon.

Australocypris robusta De Deckker, 1974

1974 *Australocypris robusta*: De Deckker, 1974

Diagnosis: Chitinous pocket on inside of posterodorsal area in female valves; hemipenis with digitate lateral lobe which is of about same width all along.

Ecology and distribution: The salinity range of *A. robusta* in Victoria, already available in Bayly & Williams (1966), of 53.5–93.1‰ and of 4.4–132‰ in Geddes (1976) is broadened to the range of 7–145‰ obtained from collections made in many lakes in January 1980. This particularly broad range was not reached by specimens of the same species in lakes in the Coorong area of South Australia. There the range is 15–38‰ (De Deckker & Geddes 1980). The query concerning the validity of Geddes' (1976) record of the salinity for *A. robusta* in Victoria, made by De Deckker & Geddes (1980, p. 691) is resolved since further work has demonstrated that the salinity range of *A. robusta* definitely differs between Victorian and South Australian

lakes. Similarly, Geddes (1976) could not have misidentified *A. robusta* since it is the only *Australocypris* species recorded in his study area.

In Victorian lakes, *A. robusta* is found in a healthy state and in high numbers at salinities between 45 and 77.5‰ and nearly always occurs with *Diacypsis compacta* which is found in even higher numbers. At higher salinities, these two species are found with *Platycypsisbaueri*. *A. robusta* occurs in two permanent salt lakes in Victoria, Lakes Gnotuk and Keilambete, which have salinities in the vicinity of 60‰ the whole year round. This indicates that this species does not necessarily require a sharp decrease in salinity to hatch although Geddes (1976) showed the hatching range for *A. robusta* to be 8.5–108‰.

SUBFAMILY: CYPRICERCINAE McKenzie
1971

Strandesia Vavra, 1895

Type species: *Strandesia mercatorum* (Vavra, 1895).

Strandesia phoenix n.sp.

FIGS 15 j–q, 16

Diagnosis: *Strandesia* without shell ornamentation, with left valve larger than right valve all along and overlapping it ventrally, except in the anterodorsal area at the extremity of the hinge, where it is overlapped by the right valve; ellipsoid in lateral view and oval with pointed end in dorsal view. Valves asymmetrical when viewed from anterior: greatest extension of right valve at about 0.33 of height from dorsum and of left valve at 0.66.

Description: *Carapace.* (External) Pseudopunctate ellipsoid shell with dorsum and ventrum gently curved, anterior slightly more rounded than posterior which tapers gently; in dorsal view oval with both ends pointed; in anterior view, valves asymmetrical: greatest extension of right valve at about 0.33 of height from dorsum and of left valve at 0.66. Left valve larger than right all along and overlapping it ventrally except in anterodorsal area at extremity of hinge where it is overlapped by right valve normal pores of simple type, some rimmed, others funnel-shaped.

(Internal) Inner lamella broadest anteriorly and almost absent posteriorly in both valves; in left valve flange broad all along except dorsally; inner lamella near outer margin perpendicular to flange in anterior of left

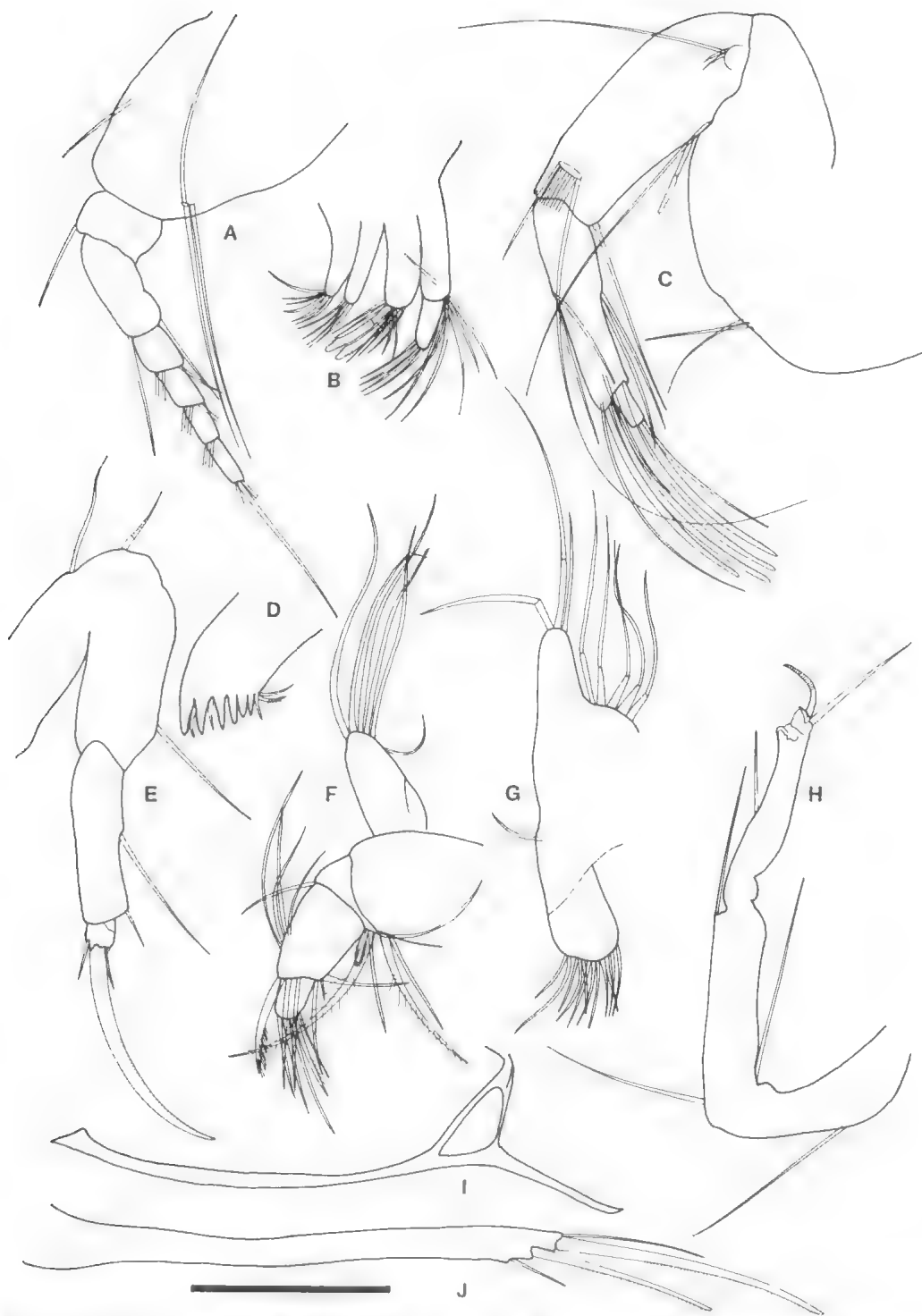


Fig. 16. *Strandesia phoenix* n.sp. a antennula, b maxillula—palp and lobes, c antenna, d mandible—coxale, e thoracopoda I, f mandible—palp, g maxilla, h thoracopoda II, i furcal attachment, j furca. a-j: holotype adult female. Scale: 100 μ .

valve and curved inward in its middle; this flat area met by broad selvage of right valve; selvage faint and peripheral in left valve and broad all along in right valve.

Anatomy: Antennula: (Fig. 16a) 7-segmented; length/width ratio of last six segments: 1/1.8, 1/4, 1/1, 1.6/1, 2/1, 3/1; natatory setae as long as last six segments together.

Antenna: (Fig. 16c) Four almost equal claws: three on penultimate segment and one on distal segment; natatory setae extending past tip of claws.

Mandible: (Figs 16d,f) Mandibular coxale with seven teeth; distal tooth acicular; epipod with five long and one short Strahlen; distal segment of palp rectangular and with long, slim and barren α bristle, β bristle stout and pilose, γ bristle thick and twice length of distal segment and pilose on inside of its distal half. Rake-like organ: Six teeth plus one bifid on inside of each rake.

Maxillula: (Fig. 16b) Length/width ratio of palp segments: 3/1, 3/1; two toothed Zahnborsten on 3rd lobe.

Maxilla: (Fig. 16g) Middle seta more than twice length of other two which are of almost equal length.

Thoracopoda I: (Fig. 16e) First segment with two unequal setae, distal one pectinate and 0.5 length of other; 3rd segment undivided in middle where long seta occurs.

Thoracopoda II: (Fig. 16h) Distal pincers large and distal setae unequal: shortest one curved, with distal half comb-like and 0.5 length of other smooth one; middle seta on last segment less than 0.5 length of all other setae which are of similar length.

Furca: (Fig. 16j) Very long furcal shaft, twice length of longest claw; anterior seta more than twice length of other seta furcal attachment: Median branch narrow and gently curved (fig. 16j) dorsal branch forming eyelet whereas ventral branch straight.

Colour of shell: Purple.

Size:

holotype adult female

	L	H	I	H
I.V	840 μ	510 μ	RV	860 μ
				540 μ

Type locality: Coastal dune lake at Evans Head, southwest of Lismore, N.S.W. (29°06' 57"S, 152°25'40"E).

Derivation of name: From Greek *phoenix* (= purple) for the colour of the shell.

Ecology and distribution: *S. phoenix* has only been collected from the type locality. Water was fresh. No males have been found and no sperms were noticed in the ovigerous females, suggesting that the species was parthenogenetic at that locality.

SUBFAMILY: DIACYPRIDINAE McKenzie, 1978

Reticypris McKenzie, 1978

Type species: *Reticypris herbsti* McKenzie, 1978.

Discussion: *Reticypris* is an Australian endemic genus which groups the following halobiont species: *R. herbsti* McKenzie, 1978, *R. walhu* De Deckker, 1979, *R. clava* n.sp. and *R. kurdimurka* n.sp. *R. dedeckkeri* McKenzie, 1978, has been synonymized to *R. herbsti* by De Deckker & Geddes (1980) as both taxa have an identical hemipenis (see discussion below). All *Reticypris* species, which are easily distinguishable from one another by the outline of the hemipenis, are discussed below.

***Reticypris clava* n.sp.**

FIGS 17-18

1980 *Reticypris* sp.nov.1, De Deckker & Geddes, p. 692.

Diagnosis: *Reticypris* with lateral lobe of hemipenis crescentic and broadest at base where two lumps are visible on inner side.

Description: **Carapace.** (External) Subrectangular with dorsum gently arched and ventrum almost flat except in mouth region which is concave; anterior broadly rounded and posterior tapering with posterodorsal area inclined; slight depression at extremity of hinge anteriorly; left valve slightly larger all along and overlapping right valve in mouth region dorsally, especially where slight depression occurs; surface of shell with small, dense reticulation usually all over and thickness of reticulation variable; outer flange close to outer margin, narrow and thinly denticulated except in mouth region where it is straight; greatest height at about 0.4 from anterior; in dorsal view like a flattened oval and both extremities slightly pointed. Normal pore canals of simple type and rimmed.

(Internal) Inner lamella equal in both valves and broadest anteriorly, tapering to 0.66 of the width posteroventrally. Hinge consists of broad

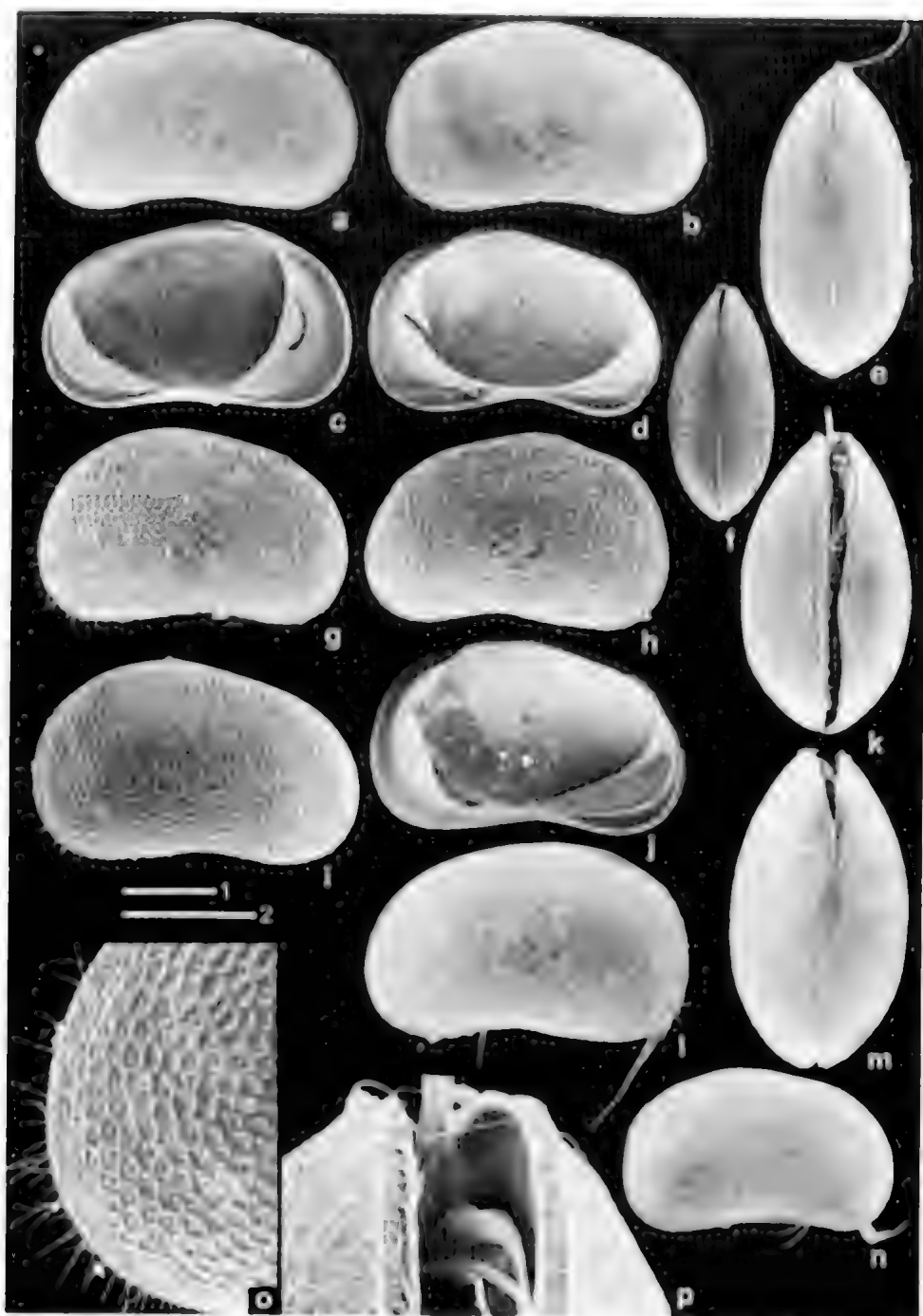


Fig. 17. *Reticypris clava* n.sp. a RV external, b LV external, c LV internal, male paratype. d RV internal, male paratype. e C dorsal, male paratype. f C dorsal, male. g LV external, female paratype. h RV external, female paratype. i LV external, female paratype. j RV internal, female paratype. k C ventral, female paratype. l C showing RV, female paratype. m C dorsal, female paratype. n C showing LV, male. o LV external, anterior detail of i. p C ventral, anterior detail of k. a-e, g-m, o-p: Type locality; f, n: Lake Weeranganuk, Vic. Scale: 1—200 μ for a-n; 2—100 μ for o;—50 μ for p.

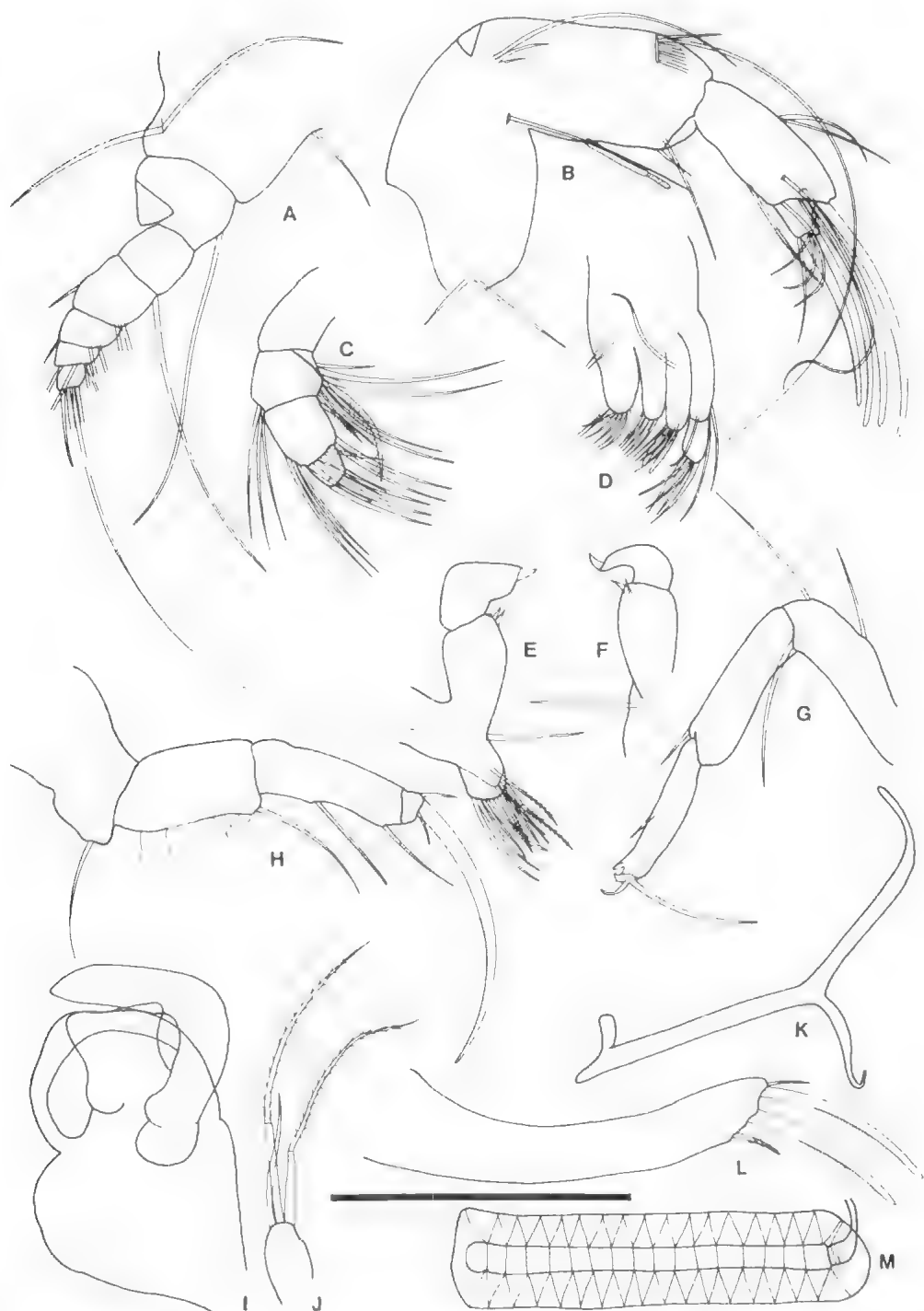


Fig. 18. *Reticypris clava* n.sp. a antennula, b antenna, c mandible palp, d maxillula, palp and lobes, e maxilla, male, f maxilla, endopodite, male, g thoracopoda II, h thoracopoda I, i hemipenis, j maxilla—endopodite, female, k furcal attachment, l furca, m Zenker organ. a-i, k-m: holotype adult male; j: paratype adult male. Scale: 100 μ .

groove in left valve in which interlocks right valve; radial pore canals numerous and straight.

Anatomy: Antennula: (Fig. 18a) 7-segmented; length/width ratio of last six segments: 1/1.5, 1/1, 1/1, 1/1.8, 1/2, 1/1; natatory setae slightly longer than all segments together.

Antenna: (Fig. 18b) Three long and equal claws on penultimate segments with shorter claw on distal one which is pectinate in male; natatory setae extending past tip of claws.

Mandible: (Fig. 18d) Seven teeth on mandible coxale; last one longer than other three adjacent to it and, near its base, two short pilose setae; length/width ratio of palps: 4.5/1, 1.7/1; 3rd lobe has two smooth Zahnborsten; epipod with five plumose Strahlen and a smaller barren one.

Rake-like organ: Eight teeth with an additional bifid one on inner side.

Maxillula: (Fig. 18c) Distal segment squarish; α , β and γ bristle of equal length and slim; α smooth, β pectinate, γ smooth.

Maxilla: Sexually dimorphic; in male, palps asymmetrical (Figs. 18e,f): broadest forming right angle on outside whereas other more arched; in female (Fig. 18j) setae unequal with shortest smooth whereas other two plumose; for chaetotaxy of protopod see Fig. 18e.

Thoracopoda I: (Fig. 18h) Penultimate segment undivided and all inner setae long and of about equal length.

Thoracopoda II: (Fig. 18g) Distal pincers small and distal setae unequal; shorter one curved and 0.25 length of other.

Hemipenis: (Fig. 18i) Lateral lobe crescent-shaped and broadest at the base where two lumps are visible on inner side; inner lobe squarish with three sides concave.

Zenker organ: (Fig. 18m) Elongated with 16 rosettes.

Furca: (Fig. 18l) Pectinate claws thick and equal; setae equal, pectinate and 0.33 length of claws.

Furcal attachment: (Fig. 18k) Median branch straight and of about same length as curved inward dorsal branch; ventral branch forming obtuse angle with dorsal one and hook-shaped distally; short rod-like, extension at right angle on base of median branch.

Eye: Cups of nauplius eye fused.

Colour of shell: Light green to white.

Size

holotype adult male

	L	H		L	H
LV	700 μ	430 μ	RV	590 μ	430 μ

paratype adult female

	L	H		L	H
LV	720 μ	445 μ	RV	700 μ	440 μ

Type locality: Ephemeral salt lake S of the Coorong Lagoon, S.A. (36°13'36"S, 139°41'29"E) = locality 3 of De Deckker & Geddes (1980).

Derivation of name: From Latin *clava* (= club) for the diagnostic shape of the outer lobe of the hemipenis

Ecology and distribution: In collections from western Victorian lakes, *R. clava* was always accompanied by low salinity ostracods such as *Mytilocypris splendida* or *M. praeununcia*, and occasionally with *D. spinosa*. Salinity for these collections ranged between 4 and 42‰. In the lakes adjacent to the Coorong Lagoon in South Australia, the salinity range for *R. clava* is 5–131‰ but it was never found in high numbers above 68‰. Only in one lake near the Coorong Lagoon (locality 7 of the De Deckker & Geddes 1980) was *R. clava* found together with *R. herbsti*—this co-occurrence persisted throughout the year, *R. clava* has been collected once in Western Australia between 14.6 and 59.5‰ (Geddes *et al.* 1981).

Remarks: It is difficult to distinguish *R. clava* and *R. herbsti* on features of the shell as reticulation of the shell and even shape and size are known to vary (see Fig. 17 for *R. clava*). The outline of the hemipenis is a good diagnostic feature for separation of the two species

Reticocypris herbsti McKenzie, 1978

1978 *Reticocypris herbsti* n.sp., McKenzie, p. 188.

Diagnostic: *Reticocypris* with lateral lobe of hemipenis boot-shaped

Description: See McKenzie (1978), p. 188–9.

Ecology and distribution: *R. herbsti* is tolerant to higher salinities than *R. clava*. In western Victorian lakes it was found with *D. compacta* at salinities between 99 and 172‰, whereas, in the lakes near the Coorong Lagoon, it occurred at salinities between 12 and 141‰ with three supplementary records at 195, 216 and 218‰. It is found in high numbers between 104 and 124‰ salinity.

In a number of specimens, collected in lakes near the Coorong Lagoon, specimens with thin

and faintly reticulated shell were seen, whereas others were thicker with a coarse reticulation. Similarly, a ventral ridge was occasionally associated with a coarsely reticulated shell, or also with juveniles. The ecological significance of these differences is not known.

***Retieypris kurdimurka* n.sp.**

FIGS 19–20

Diagnosis: *Retieypris* with outer lateral lobe of hemipenis spout-shaped and copulatory sheath heart-shaped.

Description: *Carapace.* (External) Subrectangular to squarish in lateral view with both valves usually thick; reticulation resembles broad punctation; anterior and posterior similar and broadly rounded; ventrum flat except in mouth region where it is concave; dorsum arched or depressed in front of point of greatest height, and at 0.33 from anterior, and behind it, it slopes gently; outer lamella thin and peripheral; left valve slightly larger all around and in some specimens overlap of left valve over right one is obvious, at both extremities of the hinge, as it forms smooth elongated humps.

(Internal) Inner lamella slightly broader anteriorly compared to posteroventral area; selvage faint and peripheral in right valve whereas at a distance from outer margin in left valves; radial pore canals narrow and straight; hinge consists of a broad groove in left valve in which right valve interlocks.

Anatomy: *Antennula:* (Fig. 20a) 7-segmented length/width ratio of last six segments: 1/1.25, 1/1, 1/2.5, 1/2, 1/2, 1/1; natatory setae longer than all segments together.

Antenna: (Fig. 20b) Three equal long claws on penultimate segment; 4th claw on distal segment reaching tip of other claws and pectinate in male, whereas it is shorter and with smaller teeth in female; natatory setae reaching tip of claws.

Mandible: (Fig. 20h) Mandibular coxale with seven teeth; palp with distal segment squarish, α bristle short, slim and smooth β bristle short, stout and pilose, γ bristle twice length of distal segment and pilose in its distal half.

Rake-like organ: Eight teeth with an additional inner one which is bifid.

Maxillula: (Fig. 20c) Distal palp almost squarish and 3rd lobe with two smooth Zahnhorsten.

Maxilla: Sexually dimorphic: in male (Figs

20e,f) almost symmetrical: one slightly more arched and narrower than other; in female (Fig. 20g) three smooth setae, middle one being more than twice length of other two which are equal.

Thoracopoda I: (Fig. 20d) 3rd segment undivided; inner setae small and unequal.

Thoracopoda II: (Fig. 20i) As for *R. clava*.

Hemipenis: (Figs. 20k,l) Lateral lobe spout-shaped and broadest at mid-length; copulatory sheath heart-shaped.

Zenker organ: (Fig. 20n) Elongated with 11 rosettes.

Furca: (Fig. 20m) Claws equal and thick; setae equal and small, about 0.25 length of claws.

Furcal attachment: (Fig. 20j) Median branch and long dorsal one gently curving; ventral branch forming a right angle with dorsal branch and forming a loop distally; vertical rod-like extension near base of median branch.

Eye: Cups of nauplius eye fused.

Colour of shell: White when preserved in alcohol.

Size:

holotype adult male

	I	H	L	H
LV	565 μ	350 μ	RV	560 μ

paratype adult female

	I	H	L	H
LV	600 μ	400 μ	RV	590 μ

Type locality: Madigan Gulf, Lake Eyre, South Australia.

Derivation of name: *Kurdimurka* is an aboriginal name for a legendary creature supposed to inhabit the bottom of lagoons and creeks in the Lake Eyre district.

Ecology and distribution: One specimen of *R. kurdimurka* had been originally collected from Lake Eyre North on 28.IV.1975 at about 40‰ salinity when the lake was last flooded (see Bayly 1976, p. 664 where it is referred to as "undescribed cypridid genus"). Subsequently, it has been collected twice from Madigan Gulf, at Lake Eyre by W. Zeidler on 11.XII.1974 and 2.XII.1975—no salinity records for these collections are available. Recently, the same species was collected from Lake Annean, 40 km S of Meekatharra, in W.A., at 21.3‰ salinity (see Geddes *et al.*, in press). The Western Australian specimens had a much thinner shell than those from Lake Eyre.

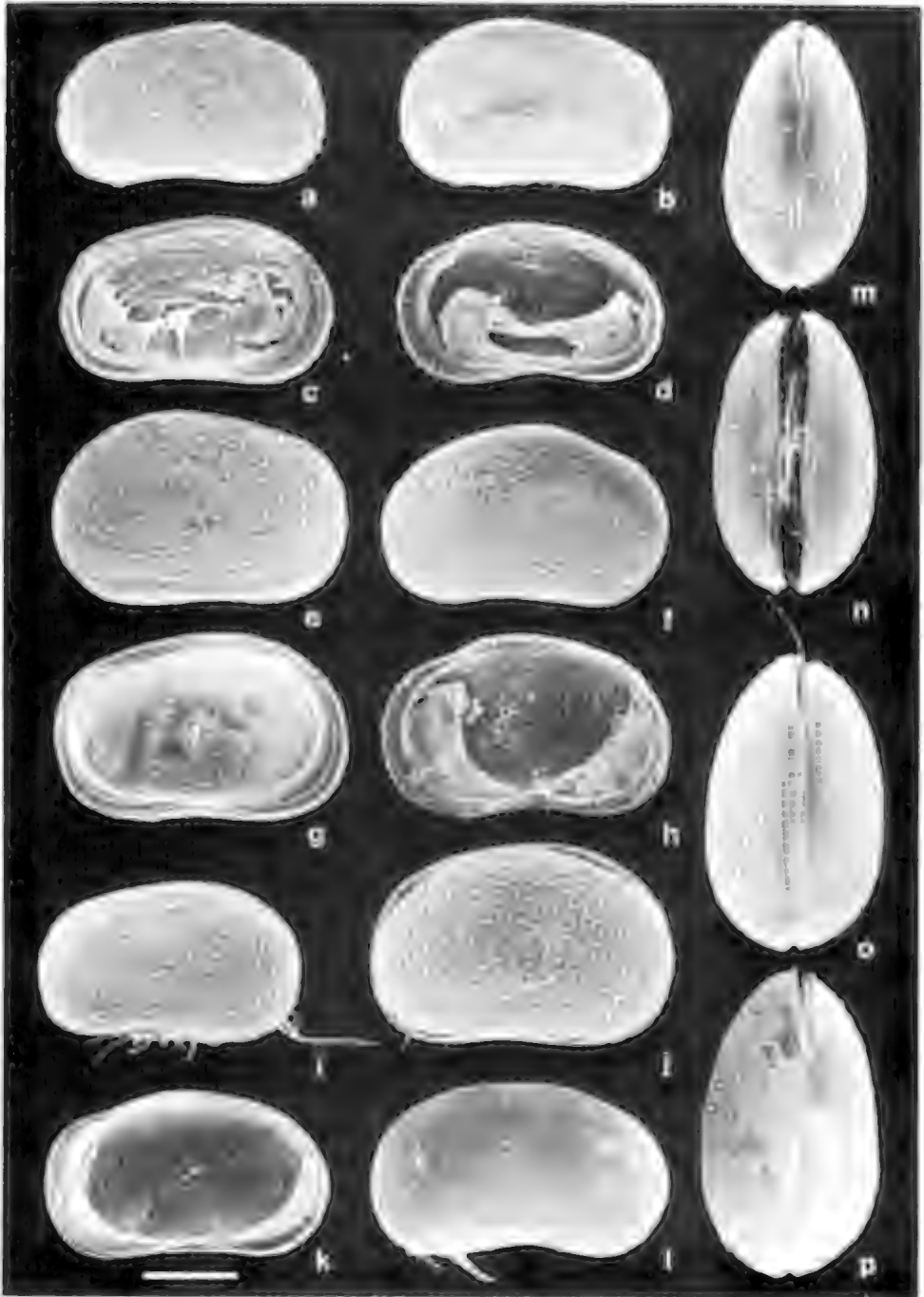


Fig. 19. *Reticypris kurdimurka* n.sp. a RV external, male holotype. b LV external, male holotype. c LV internal, male paratype. d RV internal, male paratype. e LV external, female paratype. f RV external, female paratype. g LV internal, female paratype. h RV internal, female paratype. i C showing RV, male paratype. j C showing RV, female paratype. k RV internal, male. l C showing LV, male. m C dorsal, male paratype. n C ventral, male paratype. o C dorsal, female paratype. p C dorsal, male. a-j, n-o: Type locality; k-l, p: Lake Annean, 40 km S of Meekatharra, W.A. Scale: 200 μ .

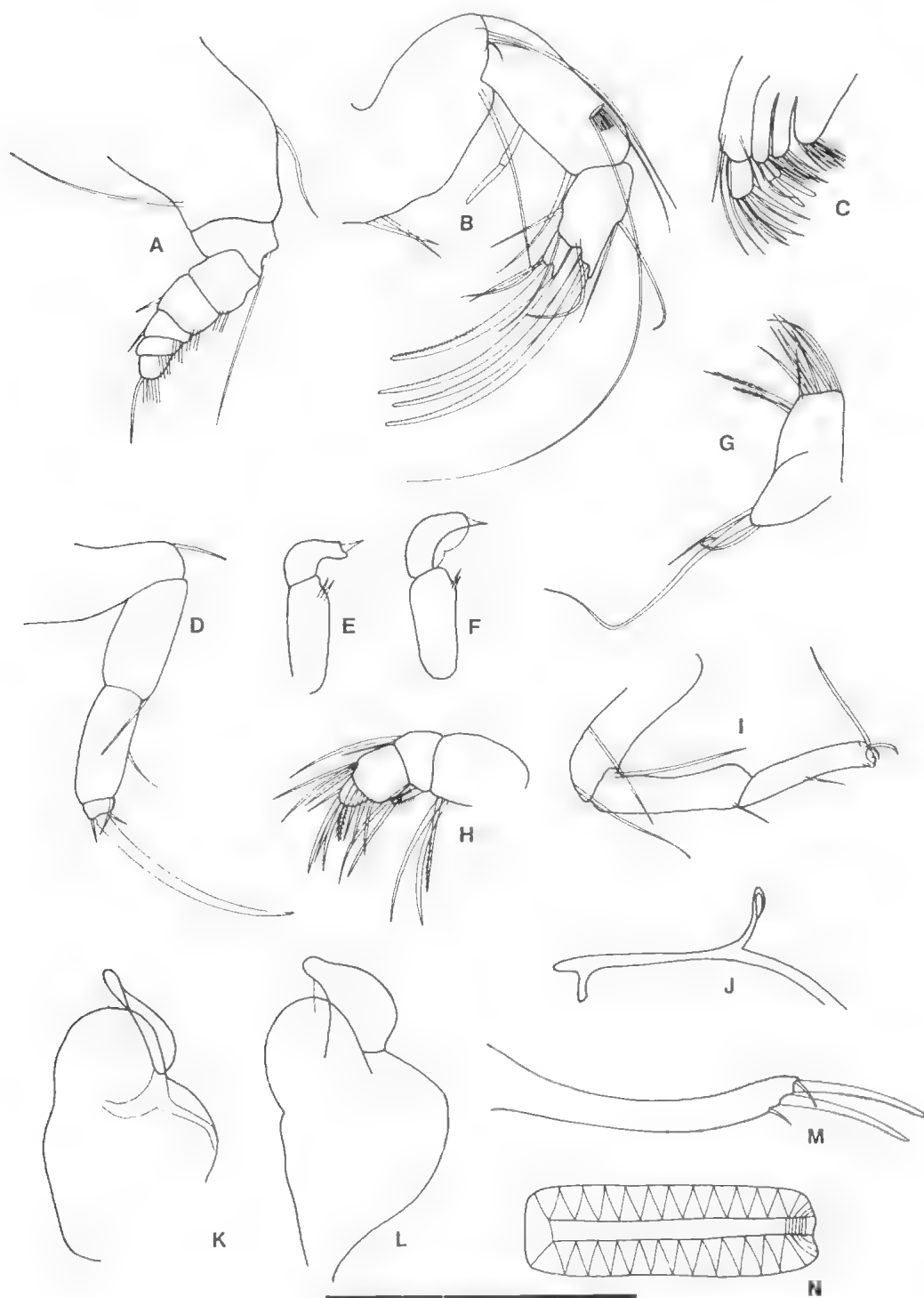


Fig. 20. *Reticypis kurdinurka* n.sp. a antenna, b antennula, c maxillula—palp and lobes, d thoracopoda I, e maxilla—endopodite, male, f maxilla—endopodite, male, g maxilla, female, h mandible—palp, i thoracopoda II, j furcal attachment, k hemipenis, l hemipenis, m furca, n Zenker organ. a-b, d-f, h-n: holotype adult male; c, g: paratype female. Scale: 100 μ .

Retiocypris walbu De Deckker, 1979

1979 *Retiocypris walbu* De Deckker, p. 162.

Diagnosis: *Retiocypris* with lateral lobe of hemipenis banana-shaped and inner lobe eudgel-shaped.

Description: See De Deckker (1979) p. 162-4.

Discussion: *R. walbu* was originally described from samples collected in mound springs between Strangways and Curdimurka, near Lake Eyre South in South Australia. Since then it has been recognized from a collection made by I. A. E. Bayly and W. D. Williams in Lake Buchanan, S.W. of Charters Tower in Queensland, in January 1965. Water salinity was 87.6‰ (Bayly & Williams 1973). It has not been found in subsequent collections made at the same lake by B. V. Timms. Similarly, it is surprising that *R. walbu* has not been collected in Lake Eyre instead of *R. kurdimurka*. Such patchy distribution remains unexplained.

FAMILY: ILYOCYPRIDIDAE Kautmann,
1900

Ilyocypris Brady & Norman, 1889

Type species: *Ilyocypris gibba* (Ramdohr, 1808).

Ilyocypris australiensis Sars, 1889

1889 *Ilyocypris australiensis* Sars, p. 46.

FIG. 21

Diagnosis: *Ilyocypris* with club-shaped inner lobe on hemipenis extending to as much as 0.66 of length of trapezoid lateral lobe.

Remarks: The original description of *I. australiensis* by Sars (1889a) is sufficient, and does not warrant additional illustrations of the anatomy here. The ornamentation and outline of the valves of *I. australiensis*, however, are extremely variable. Typical variations are illustrated in Fig. 21 (all SEM photos are at the same scale and only adults are represented). The surface of the shell can be finely (Fig. 21i) to coarsely pitted (Figs 21e,f,o); acicular but small spines occur, mostly posterodorsally (Figs. 21h,i) when present, but can also cover the entire carapace (Fig. 21a). The outline of the shell is also variable anteriorly and dorsally. In dorsal view, anteriorly the shell can be pointed (Figs 21j,o) or with a squarish blunt end (Figs 21m,n). The latter feature is often accompanied by a depression bordering the periphery of the valve anteriorly and posteriorly (Figs 21a,d). De-

pressions are also variable dorsally; a circular one above the central muscle field and the other vertical above and in front of the central muscle field.

The ecological significance of all these variations are not yet understood but this is not a surprising phenomenon since *I. australiensis* is commonly found in temporary pools which are renowned as the sites of broad variations in physical parameters (viz. temperature, pH, O₂). *I. australiensis* can swim but is usually found crawling in or above muddy substrates in ponds. The species usually occurs in ponds which retain water for a few months and which have a very soft substrate. *I. australiensis* has also been collected in a number of shallow and slightly saline lakes in western Victoria. These lakes are characterized by small fluctuations in salinity over the year. This explains the absence of *I. australiensis* in the saline lakes near the Coorong Lagoon studied by De Deckker & Geddes (1980) where salinity of some lakes was close to fresh in winter, but rose rapidly during spring and summer months. In western Victoria, the range of salinity tolerance of *I. australiensis* is usually 4-7‰, with one record at 10.37‰ in Lake Kariah. So far, *I. australiensis* has never been collected in deep lakes (fresh or slightly saline) nor in permanent fresh lakes.

I. australiensis has been collected all across Australia. It is also recorded from North Africa (Gauthier 1928), Asia and southern Europe (Hartmann 1964, p. 148).

As the morphology of the hemipenis of *I. australiensis* and *I. decipiens* Masi, 1906, as illustrated in Petkovski (1958), is almost identical, it is suggested here that these two species could be synonymous. Further work is necessary to confirm this hypothesis, but it is important to be aware of the variation in shell ornamentation of the *Ilyocypris* species as illustrated above, and by Diebel and Pietrzeniuk (1975) for *I. bradyi* Sars, 1890, since many *Ilyocypris* species are separated on shell morphology alone. The selection of particular features of the shell as taxonomically important by van Harten (1979) will not prove to be useful for *I. australiensis* specimens since for example, the "marginal ripples" of van Harten are variable in Australian specimens, and even occasionally absent. Further, distinction of species on features other than

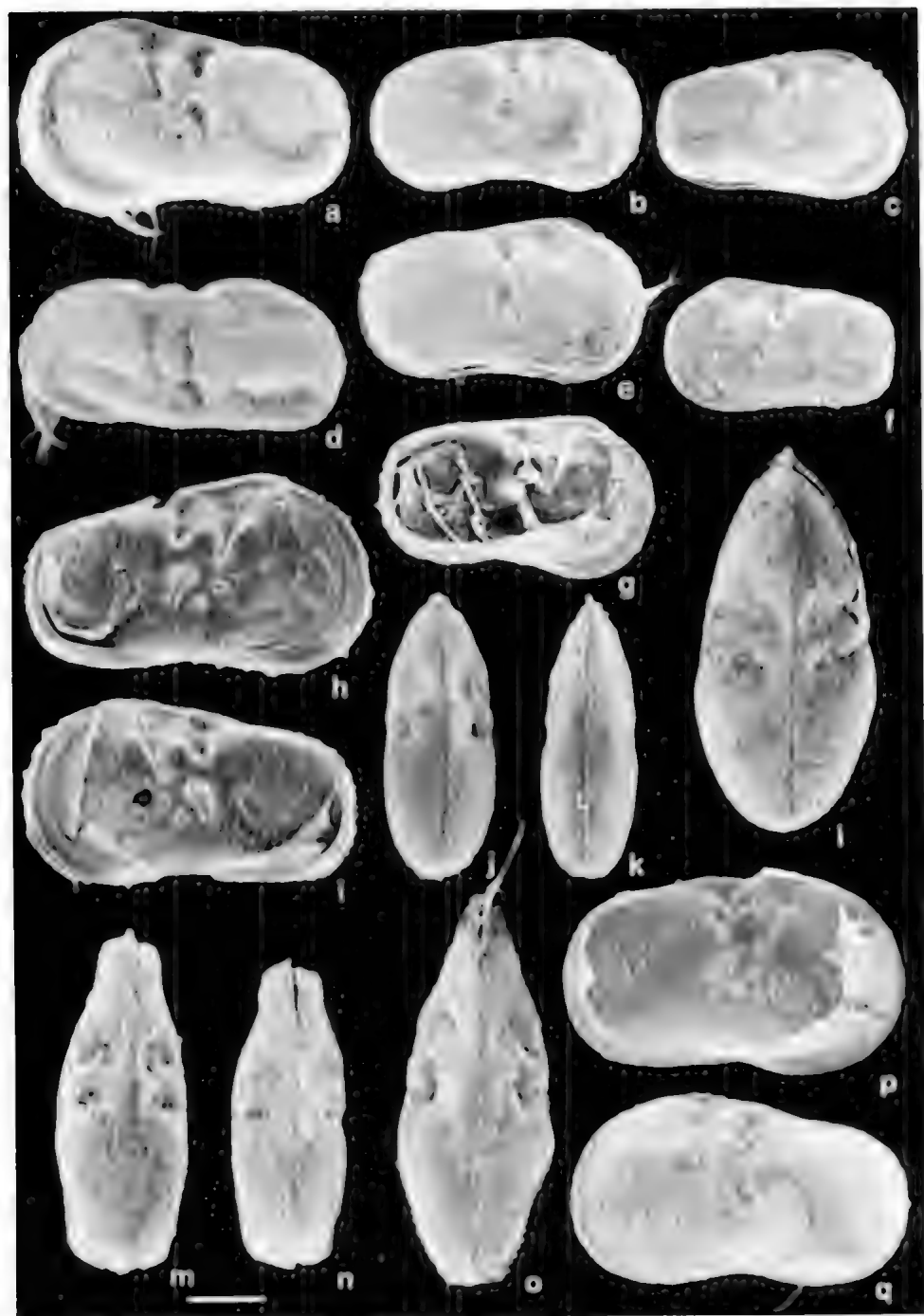


Fig. 21. *Ilyocypris australiensis* Sars, 1889. a C showing LV, female. b RV external, male. c C showing RV, female. d C showing LV at dorsolateral view, male. e C showing RV, male. f C showing LV, male. g LV internal, male. h LV internal, female. i RV internal, female. j C dorsal, female. k C ventral, male. l C dorsal, female. m C dorsal, female. n C dorsal, male, same specimen as d. o C dorsal, female. p LV internal, female. q C showing LV, male. a, d, h-i, m: Pool in creek bed at 25 km N of Cue, W.A. b, e, g, j-k: Martin Lake Vic. c, f: in vent to Warrawenia Lake, N.S.W.; l, p-q: Pool in creek bed, 12 km S of Menzies, W.A.; o: Pond very close to Reel Inlet (coastside) 19 km S of Mandurah, W.A. Scale: 200 μ .

the hemipenis is likely to be unreliable since the morphology of many appendages of *Ilyocypris* species are known to vary. For example, Gauthier (1928) discussed the variations in the anatomy of *I. australiensis* and *I. biplicata* (Koch, 1838) from North Africa and concluded that he was incapable of separating the species, although neither was he prepared to synonymize them.

Ilyocypris perigundi n.sp.

FIGS 22-23

Diagnosis: *Ilyocypris* with carapace trapezoid; anterodorsal area at hinge extremity compressed and forming a hump when viewed laterally; three large protuberances in dorsal area, posterior one being largest, pustulose and ending with a number of wart-like tubercles; ventrum concave and at 0.6 from anterior. Club-shaped inner lobe of hemipenis reaching tip of trapezoid lateral lobe.

Description: *Carapace.* (External) Trapezoid with greatest height 0.2 from anterior where hinge starts; dorsum straight except at point of greatest height where both valves form flattened hump; ventrum concave at 0.6 from anterior. Surface of shell highly ornamented; three protuberances dorsally with posterior one largest and ending with broad wart-like tubercles from which seta protrudes; below posterior protuberance and above ventrum, is an additional highly ornamented protuberance; this is point of greatest width of shell; deep depression dorsally between middle and posterior protuberances; shell covered with broad pseudopunctae which are pustulose inside; pointed tubercles along margin anteriorly and posteriorly. Dorsally, shell like flattened ellipsoid with anterior compressed and pointed for width of inner lamella but tapering posteriorly.

(Internal) Inner lamellae twice as wide in anterior compared to posterior in both valves; narrow selva at 0.66 from outer margin anteriorly and peripheral to inner margin posteriorly; marginal ripples broad in left valve posteroventrally.

Anatomy: Antennula: (Fig. 23e) 6-segmented; length/width ratio of last five segments: 5/3, 1.2/1, 1.3/1, 2/1, 4/1; natatory seta as long as all segments together.

Antenna: (Fig. 23a) Natatory setae twice length of last two segments and claws together;

three long distal claws on penultimate segment plus another as long as other three on last segment with a narrower and shorter one. Mandible: (Fig. 23d) Length/width ratio of last two segments of mandibular palp: 4/3, 1/1.

Maxillula: (Fig. 23b) Distal segment of palp trapezoid and ending with three broad long setae plus two shorter ones; no Zahnborsten on 3rd lobe but setae short and stout on all three lobes.

Maxilla: Sexually dimorphic: in male (Figs. 23e,h) palps two or three-jointed with one seta at the distal end of the 1st segment; in female (Fig. 23g) non-segmented, short and narrow palp with three unequal setae. For chaetotaxy see Figs 23g,h; epipod plate with five Strahlen.

Thoracopoda 1: (Fig. 23f) Last segment undivided; all setae short.

Thoracopoda II: (Fig. 23i) 4-segmented with three distal setae, two long equal ones and 3rd about 0.66 length of others.

Hemipenis: (Figs 23j,k) Outer lobe trapezoid with inner distal end pointed which is nearly reached by long club-shaped inner lobe; outer lobe triangular with distal end rounded and slightly pinched laterally; inner lobe 0.33 length of others.

Zenker organ: (Fig. 23l) Both ends of globular and with 13 rosettes.

Furca: (Fig. 23m) Two long equal claws; posterior setae slightly longer than anterior and placed at 0.4 of length of shaft from posterior claw.

Colour of shell: Transparent white.

Size:

holotype adult male					
	L	H		L	H
L.V	580µ	365µ	RV	560µ	355µ
paratype adult female					
	L	H		L	H
L.V	580µ	380µ	RV	580µ	350µ

Type locality: Warrawenia Lake, south of Menindie, N.S.W., (33°29'30"S, 141°44'30"E)
Derivation of name: From the aboriginal language *perigundi* meaning meandering lake or lagoon, as this species has been found in a lake part of an old river system (Warrawenia L.) and in a lagoon (Katarapko L.).

Ecology and distribution: This species has only been collected in three localities: Warrawenia L., Katarapko Lagoon, which is a natural billa-

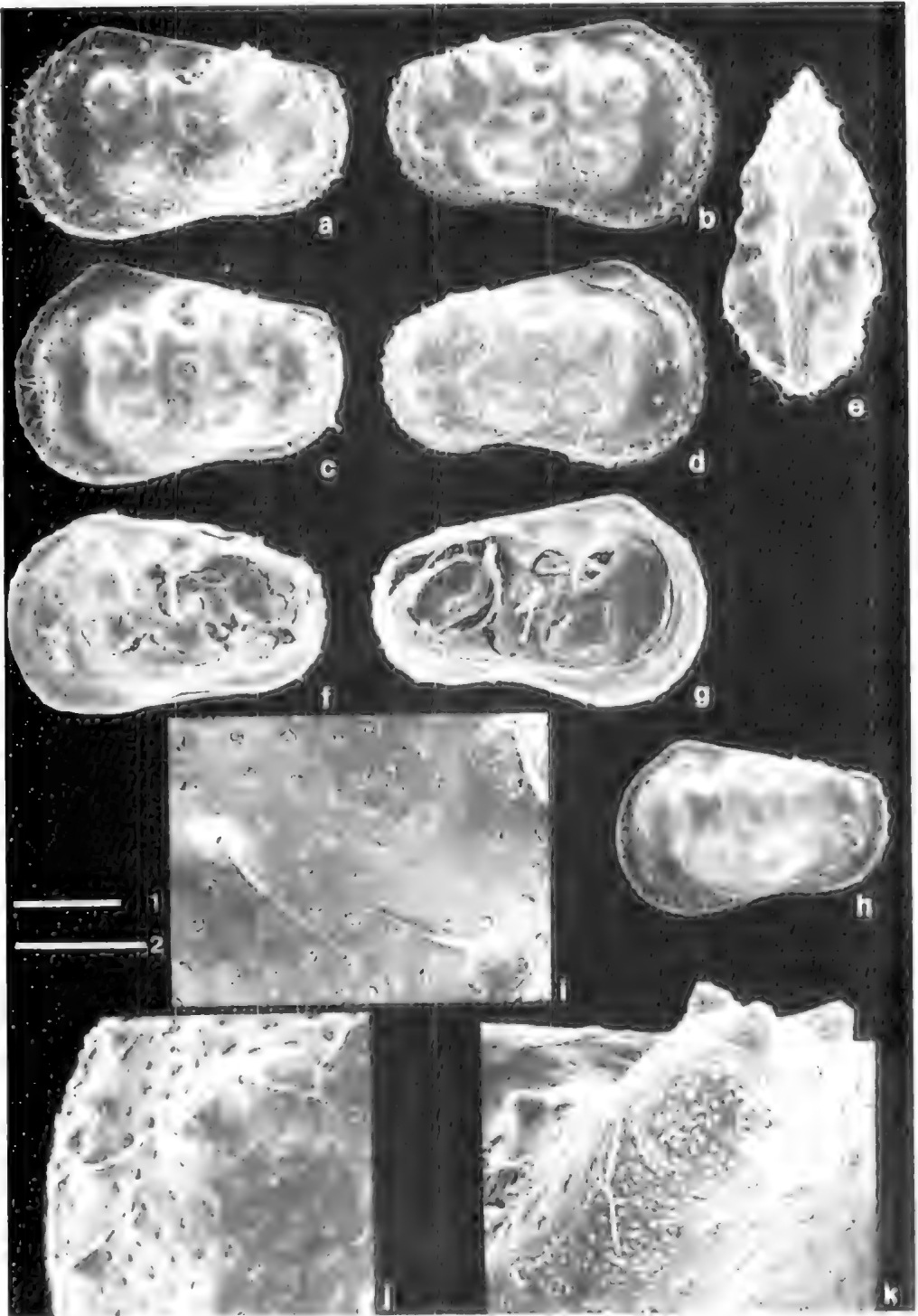


Fig. 22. *Ilyocypris perigundi* n.sp. a LV external, female paratype. b RV external, female. c LV external, female. d external, male holotype. e C dorsal, female paratype. f RV internal, female paratype. g LV external, male holotype. h LV external, juvenile. i LV external, detail of a. j LV external, posterior detail of C. k LV external, dorsal detail of a. a,d-g, i-k: Type locality; b-c, h: Katarapko Lagoon, near Loxton, S.A. Scale: 1— 200μ for a-h; 2— 50μ for i-k.

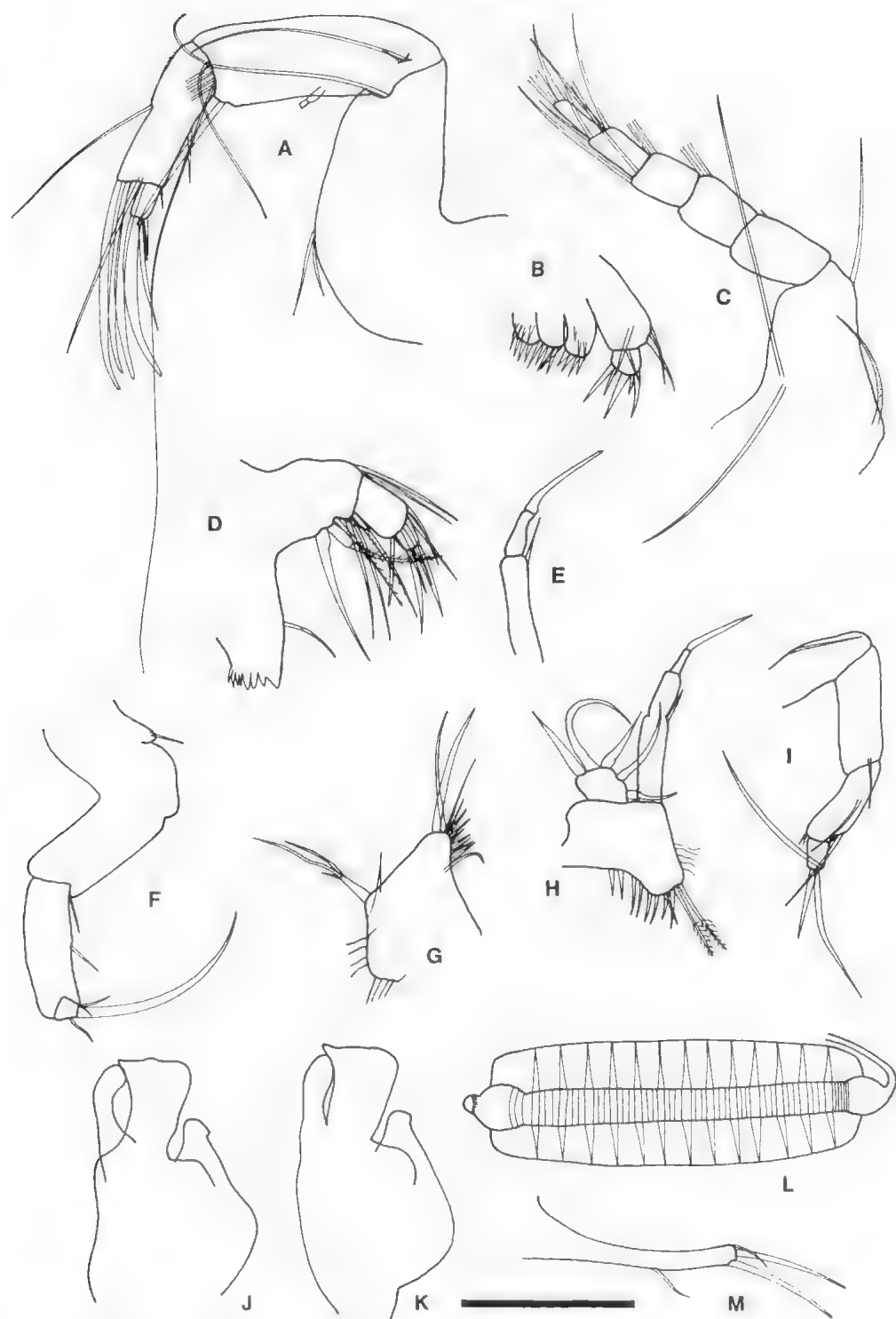


Fig. 23. *Ilyocypris perigundi* n.sp. a antenna. b maxillula—palp and lobes. c antennula. d mandible. e maxilla—endopodite, male. f thoracopoda I. g maxilla, female. h maxilla, male. i thoracopoda II. j hemipenis. k hemipenis. l Zenker organ. m furca, a-f, h-m: holotype adult male. g: paratype adult female. Scale: 100 μ .

bong converted into an evaporative basin near the River Murray at Loxton, S.A., and from Scott Creek, near Adelaide. At all three localities only a few specimens have been collected; most specimens were coated with mud particles. The salinity at Katarapko Lagoon was 3‰. Salinity of the water from the type locality has not been measured. At Scott Creek, water was fresh.

Remarks: *I. perigundi* differs from *I. australiensis* on the following features; the former is smaller and has a very different shell architecture characterized by the three highly ornamented dorsal protuberances, a ventrum placed at 0.66 from the anterior of the shell and a flat dorsal hump in the extremity of the hinge anteriorly. The inner lobe of the hemipenis in *I. perigundi* is almost as long as the lateral lobe whereas it is only 0.66 the length in *I. australiensis*.

SUPERFAMILY: CYTHERACEA Baird, 1850
FAMILY: LEPTOCYTHERIDAE Hanai, 1957

Leptocythere Sars, 1925

Type species: Leptocythere pellucida (Baird 1850)

Leptocythere lacustris n.sp.

FIGS 24-25

1919 *Cythere lubbockiana* Brady: Chapman, p. 29.

Diagnosis: *Leptocythere* with deeply pitted external surface of shell, large circular depression posteroventrally outside and where inner lamella is broadest on inside; posterodorsally near termination of hinge, shell is slightly concave and posterior to it; shell thick and smooth especially in left valve. Outline of hemipenis as in Figs 25j,k.

Description: *Carapace.* (External) Subrectangular shell, coarsely pitted and with at least two elongated grooves; anterior straight and forms an obtuse angle with hinge line and other, at posterior, runs almost parallel to curvature of shell; a deeper and broader notch often visible in posteroventral area in both valves; ornamentation of shell varying from fine to coarse ribbing; dorsum almost straight and inclined except in postero-dorsal area, just before termination of hinge where it is slightly concave; behind this, shell thick and smooth, especially in left valve; greatest height at about 0.25 from anterior; mouth region concave and at 0.4 from anterior. In dorsal view, shell com-

pressed and has almost straight sides except where grooves occur anteriorly and posteriorly; hinge area almost smooth externally.

(Internal) Inner lamella broad and widest in posteroventral area opposite external deep notch; selvage faint and peripheral in both valves; hinge crenulated all along with broad tooth at both ends in right valve and matching sockets in left one; behind anterior socket in left valve, are two smaller teeth and in front of the posterior socket, with a matching depression in right valve, is also a small tooth; central muscle field with vertical row of four scars; two in middle are elongated and parallel to hinge line whereas others are almost circular.

Anatomy: Antennula: (Fig. 25a) 6-segmented; length/width ratio of last four segments: 1.6/1, 1/1.4, 1/1 to 1.4/1, 4/1; distal thick seta pectinate.

Antennae: (Fig. 25b) Two smooth distal claws on terminal segment slightly shorter than inner claw near distal end of penultimate segment.

Mandible: (Figs 25d,e) Mandibular coxale with seven teeth and long acicular seta on inner side near base of smaller tooth; epipod with terminal segment small and square-shaped.

Maxillula: (Fig. 25c) Epipod with 14 long and short Strahlent; terminal segment of palp small, rectangular and with one distal seta jointed.

Maxilla: (Figs 25h,i) Distal claw short and slightly curved; in female inner seta on 2nd segment pilose in its distal half (Fig. 25i) whereas barren in male (Fig. 25h).

Thoracopoda I: (Fig. 25f) Slightly larger than maxilla but with only one distal seta on 1st segment.

Thoracopoda II: (Fig. 25g) Similar but slightly larger than thoracopoda I and with distal claw more slender.

Hemipenis: See outline in Figs 25j,k.

Genitalia: See outline in Fig. 25m.

Purca: (Figs 25k,m) One long seta near hemipenis and genital organ.

End of body: (Fig. 25l) With one small seta and densely pilose

Colour of shell: Light brown.

Size:

holotype adult male

	L	H	L	H
LV	500µ	270µ	RV	490µ
				270µ

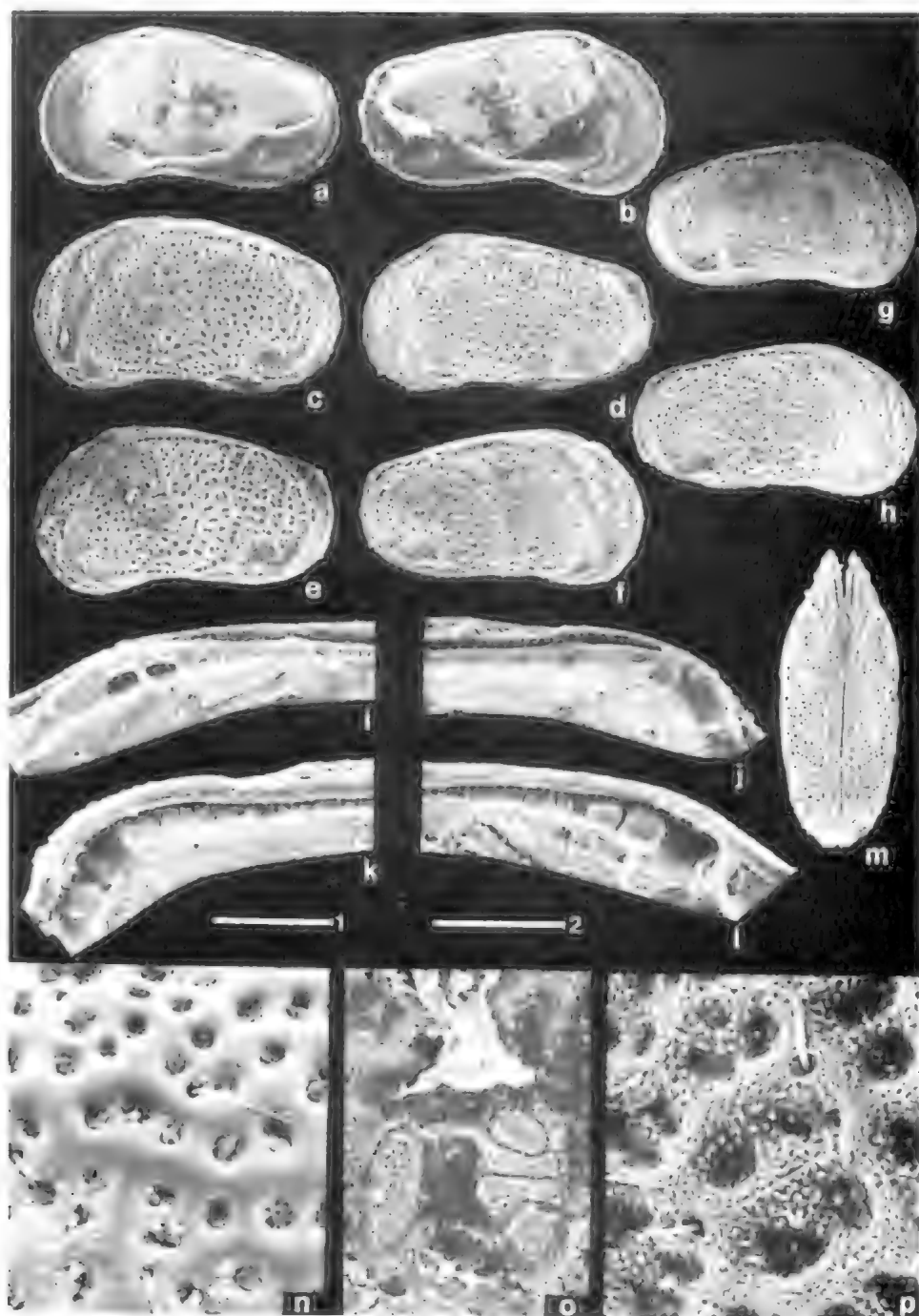


Fig. 24. *Leptocythere lacustris* n.sp. a RV internal, male holotype. b LV internal, male holotype. c C showing LV, female paratype. d LV external, male paratype e LV external female paratype. f C external showing RV, male paratype. g C external showing RV, male. h RV external, male paratype. i RV internal, hinge posterior detail of a. j RV internal, hinge posterior detail of a. k LV internal, hinge posterior detail of b. l LV internal, hinge anterior detail of b. m C dorsal, male paratype. n C external, detail of g. o RV internal, detail central muscle field of a. p LV external, detail of e, e-f, h-m, o-p: Type locality; g, n: Chara Lake, near Robe, S.A. Scale: 1—200 μ for a-h, m; 2—50 μ for i-l, o;—25 μ for n.p.

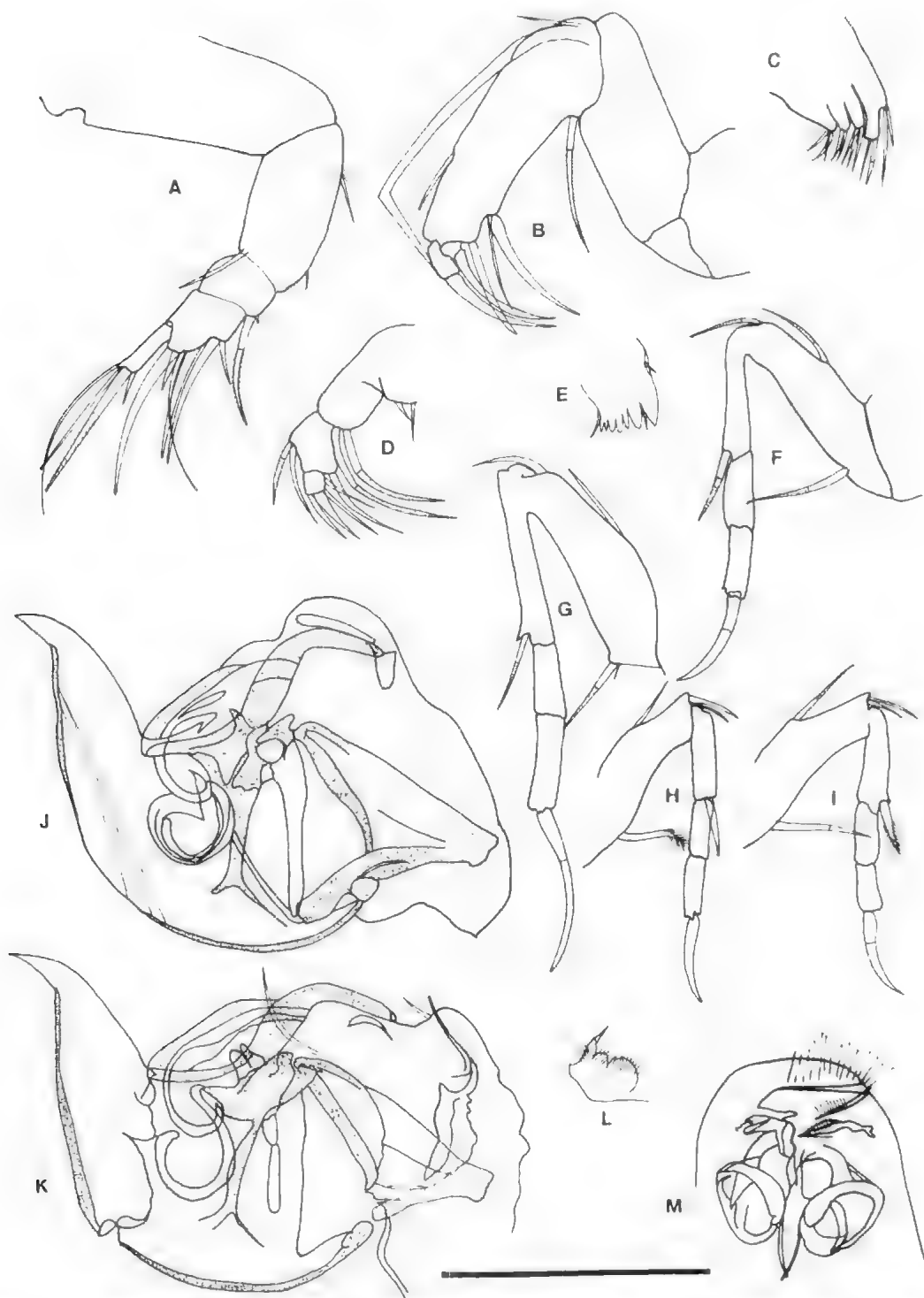


Fig. 25. *Leptocythere lacustris* n.sp. a antennula. b antenna. c maxillula—palp and lobes. d mandible—palp and lobes. e mandible—palp. f mandible—coxale. g thoracopoda I. h thoracopoda II. i maxilla, male. j maxilla, female. k hemipenis. l hemipenis. m end of body. n genitalia. a-e, g-h, j-k: holotype adult male; f, i, m: paratype adult female; l: paratype adult male. Scale: 100 μ .

paratype adult female

	L.	II	L.	II
LV	485 μ	270 μ	RV	480 μ 270 μ

Type locality: Fresh Dip Lake near Robe, S.A. (35°15'42"S, 139°48'47"E).

Derivation of name: From Latin *lacustrinus* (= of lakes) as this species, which belongs to a typically estuarine genus, is found in lakes.

Ecology and distribution: This truly benthic species has been collected in only four localities near Robe, S.A. apart from the type locality. All localities are characterized by permanent water only slight salinity fluctuations. The salinities were 19 to 28‰. In addition, at the type locality, salinity was 2.8‰. So far, *L. lacustris* has been found in permanent water around 35‰ as no such lakes have yet been sampled in the search for this ostracod. Attempts to find it in the permanent and saline lakes Keilambete and Gnotuk in western Victoria (salinity ca. 55–62‰) were unsuccessful, suggesting that the salinity range of *L. lacustris* does not reach such values. This species, as far as all others in the typical estuarine genus *Lepocythere*, is indicative of permanent water as it does not produce eggs which can withstand desiccation.

Remarks: The description of *L. lacustris* corresponds to the specimen identified by Chapman (1919) as *Cythere lubbockiana* from the fossil site at Boneo Swamp. The two rounded tubercles on the posteroventral area of the shell as illustrated by Chapman (1919) on Plate IV.9 are two sand grains which have been removed by me from the specimen in the National Museum of Victoria. The shell architecture of *L. lacustris* varies from almost smooth to coarsely reticulated (Figs 24n,p); at times, reticulation is so thick that the shell has a smooth appearance. Such variations have been mentioned for other estuarine and marine species of *Leptocythere* by Shornikov (1966) and Hartmann & Kuhl (1978). This is not surprising as environmental conditions, such as water salinity in salt lakes, can fluctuate over time.

L. lacustris is closely related to *L. hartmanni* (McKenzie 1967). Unfortunately, no males of the latter species have ever been found, as analysis of the hemipenis morphology would have confirmed this distinction. The valves of *L. hartmanni*, however, are not coarsely pitted and reticulation is more sparse (see Hartmann 1979, Pl. III; Figs 3–8). The

anterior and posterior grooves are present in both species. The posteroventral notch is much deeper in *L. lacustris* and the smooth postero-dorsal hump is absent in *L. hartmanni*.

FAMILY: LIMNOCYTHERIDAE Sars, 1925

SUBFAMILY: LIMNOCYTHERINAE Sars, 1925

Gomphodella n.gen.

Type species: *Gomphodella maia* n.sp., gender masceline.

Diagnosis: Carapace. Female carapace in dorsal view triangular with greatest width at about 0.66 to 0.75 from anterior; at about 0.4 from anterior, where central muscle field occurs, valves are slightly compressed; absence of prominent lateral ridge in ventral area; sieve pore canals and few broader normal pore canals in row parallel to posterior edge of shell in both valves. Male, in dorsal view, like a flattened oval with both ends pointed.

Anatomy: Female maxilla and thoracopodae I and II similar, although of different length; female furca with three stout, pointed and thickly pilose setae.

Derivation of name: From a combination of the two names *Gomphocythere* and *Cytheridella* as this genus shares diagnostic features of the two genera.

Remarks: *Gomphodella* is very similar to *Cytheridella* Daday, 1905 except that the shell of the former is less compressed in the area where the central muscle field occurs, and as the maxilla and thoracopodae I and II are similar in *Gomphodella* (in *Cytheridella* the thoracopoda II is transformed into a prehensile palp). The diagnostic feature which *Gomphodella* and *Gomphocythere* Sars, 1924, share is the presence of three stout and thickly pilose setae on the female furca—this is not seen in *Cytheridella*. *Gomphodella* lacks the lateral ventral ridge on both valves on the outside of the shell so typical of *Gomphocythere* species.

Gomphodella is to be included in the family Limnocytherinae Sars, 1925, following the recent regrouping of subfamilies in the Limnocytheridae by Colin & Danielopol (1978).

Gomphodella maia n.sp.

FIGS 26–27

Diagnosis: Surface of shell pseudopunctate with many sieve pores; posterior urea of shell broadly rounded in lateral view; in dorsal view,

valves only slightly compressed in female at 0.4 from anterior where central muscle field occurs. Outline of hemipenis as in Fig. 27i.

Description: Carapace. (External) Adult: Subrectangular in lateral view with ventrum flat and dorsum arched; posterior broadly rounded and anterodorsal area flatter and forming less steep angle; surface of valves pseudopunctate with many sieve pores; normal pore canals either of simple type or surrounded by rim; a few broader normal pore canals arranged in row parallel to posterior edge of shell in both valves; in dorsal view, carapace of male like flattened oval with anterior end more compressed and pointed and greatest width near middle; in female, greatest width at about 0.75 from anterior which is pointed whereas posterior almost flat except in middle which is slightly convex where both valves meet; at 0.4 from anterior, where central muscle field consisting of row of four vertical scars occurs, valves are slightly compressed in female; left valve slightly longer anteriorly and posteriorly. In some female specimens, occasional faint ridges present ventrally near outer margin of each valve and running parallel to it.

Juvenile: Almost round in lateral view with flattened ventrum; oval in dorsal view; some specimens with broad flange sometimes extending into one or two spines posteroventrally.

(Internal) Inner lamellae much broader anteriorly; selvage prominent and broad all around in both valves; in left valve, however, it is placed further away from edge of valve, especially anteriorly; in front of mouth region, selvages very broad and, when interlocking during valve closure, right selvage placed externally; shell perforated internally; radial pore canals numerous, short and usually straight. Hinge lophodont: anterior and posterior grooves in right valve elongated and matched by ridges in left valve.

Anatomy: Antennula: (Fig. 27a) 6-segmented; length/width ratio of last five segments: 1.9/1, 1.2/1, 0.8/1, 1.2/1, 3/1; longest distal seta bifid with one side more than twice length of other.

Antenna: (Fig. 27b) Three smooth distal claws on terminal segment; pectinate distal claw on inner side of penultimate segment slightly shorter than other three claws.

Mandible: (Figs. 27d,e) Mandibular coxale with seven teeth; inner one slender and twice

as long as penultimate; palp with terminal segment almost trapezoid and with two thick distal setae and a shorter and thinner one.

Maxillula: (Fig. 27c) Poorly sclerotized palp with three unequal and broad setae; epipod with 13 long and one small Strahlen.

Maxilla: (Fig. 27f) Distal claw stout, short and curved inward; setae on 1st segment smooth, and distal one on 2nd segment finely pectinated.

Thoracopoda I: (Fig. 27g) Similar to maxilla except for slightly larger size.

Thoracopoda II: (Fig. 27h) Larger than thoracopoda I with distal claw slender, longer and almost straight; inner distal end of last two segments with a short spine.

Hemipenis: Strongly chitinated; for outline see Fig. 27i.

Genitalia: For outline see Figs 27j,k.

Furca: In female (Figs 27j,k) consisting of three short, stout and pointed setae densely covered with stiff hairs and two longer and barren setae; in male (Fig. 27i), two barren setae.

Colour of shell: Grey to grey brown.

Size:

holotype adult male

	L	H		L	H
LV	490 μ	290 μ	RV	460 μ	300 μ

paratype adult female

	L	H		L	H
LV	560 μ	330 μ	RV	520 μ	320 μ

Type locality: Fresh Dip Lake, near Robe, S.A. (35°15'42"S, 139°48'42"E).

Derivation of name: From Greek *maia* meaning good mother as some adult females from fossil deposits (Pulbeena and Mowbray Swamp in Tasmania, see De Deckker 1981)⁴ were found with juveniles still inside them.

Ecology and distribution: This species only occurs in permanent waters as eggs cannot withstand desiccation (for further details, see McKenzie & Hussainy 1969). Brood care certainly occurs for this species as quite a number of female carapaces have been found to yield either one or two juveniles. It is likely to be a freshwater species which can tolerate slight concentrations of dissolved solids in the water as, like *G. australica*, it has been col-

⁴ DE DECKKER, P. (1981) Taxonomy, ecology and palaeoecology of ostracods from Australian inland waters. Ph.D. Thesis, Dept of Zoology, University of Adelaide (unpubl.).

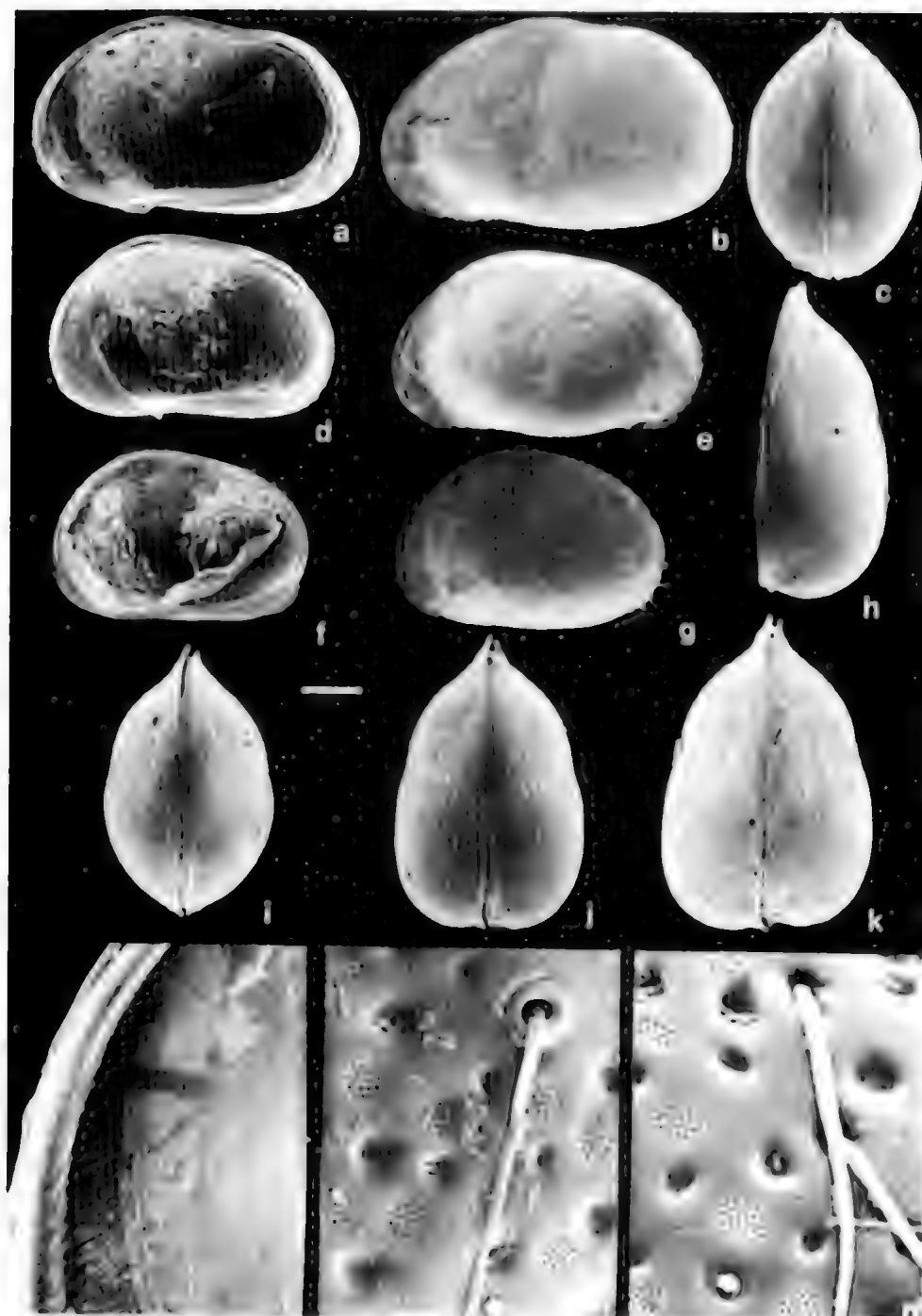


Fig. 26. *Gomphodella maia* n.gen., n.sp. a RV internal, female paratype b LV external, female paratype c C dorsal, male paratype d RV internal, male holotype. e LV external, male holotype. f RV internal, juvenile. g LV external, juvenile. h RV dorsal, female. i C dorsal, male. j C dorsal, female. k C dorsal, female. l RV internal, anterior detail of d. m LV external, detail of e. n LV external, detail of g. a-n: type locality; b-k: fossil, Blue Lake, Mt Gumbier, S.A. Scale: 1000 for a-k, 15 μ for l; 5 μ for m, n.

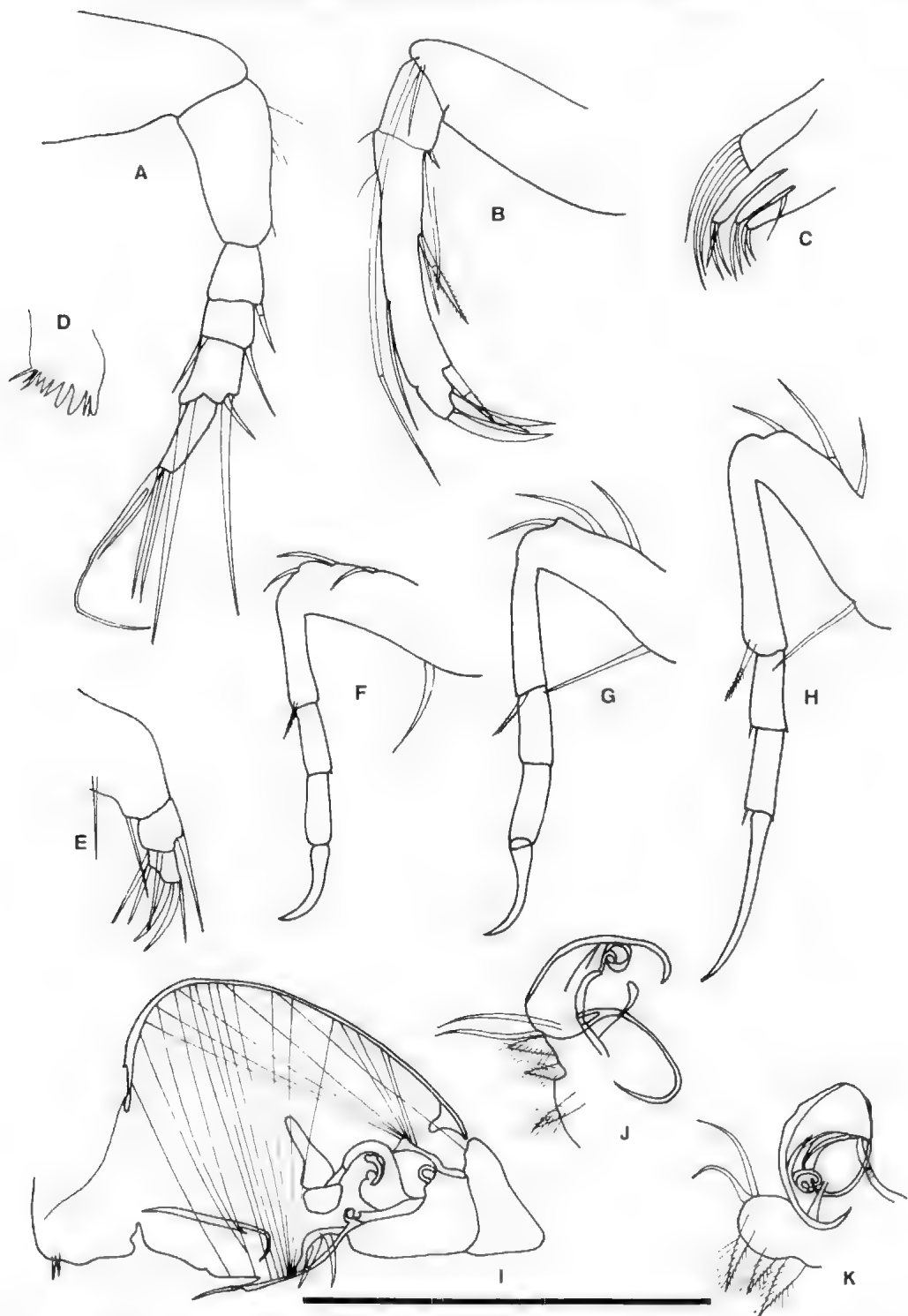


Fig 27. *Gomphodella maia* n.gen., n.sp. a antennula. b antenna c maxillula—palp and lobes. d mandible—coxale. e mandible—palp. f maxilla. g thoracopoda I. h thoracopoda II. i hemipenis and furca. j genital organ and furca. k genital organ and furca. a, c, e, j-k: paratype adult female. b, d, f-i: holotype adult male. Scale: 100 μ .

lected alive once in Fresh Dip Lake (= type locality) at 2.3‰ salinity. As a fossil, it has been found with *G. australica*, and other fresh-water ostracods in samples from a short core from the Blue Lake at Mt Gambier, S.A. It is also found in two fossil sites in northwestern Tasmania (De Deckker¹). In samples from both sites, a large number of carapaces were recovered and some of these were found with juveniles inside them. The significance of this phenomenon is not properly understood as, usually, after death under water, valves of ostracods separate prior to or during decay of the soft parts. When ponds dry up, ostracods are seen to close their valves tightly and, if this period is long enough to cause dehydration of the ostracods, death would occur. Rapid sediment accumulation is later necessary during a wet phase to prevent carapaces from opening. This process is likely to be one possible explanation for the high percentage of *G. maia* carapaces found in samples from the two Tasmanian sites. Death caused by changes in water chemistry would not prevent carapaces from dislocation. Another possibility is that *G. maia* can in fact burrow in sediment—a phenomenon noticed for a closely related ostracod *Gomphocythere* sp. (with another ostracod *Darwinula sphagna* Barclay, 1968) found in the interstitial waters of the Rotorua lakes in New Zealand by Chapman & Lewis (1976)—and, if it was to remain there until death, valves could not become easily dissociated.

Gomphodella australica (Hussainy, 1969)

1969 *Gomphocythere australica* Hussainy, p. 299

Diagnosis: Subrectangular shell with both dorsum and ventrum almost straight; anterior broadly rounded and posteroventral area more pointed with furthest extension of shell at about 0.33 from dorsum; shell ornamentation consisting of faint but broad reticulation especially at anterior and posterior ends. In dorsal view shell in female like an upside down heart and male much narrower with both ends pointed.

Size range:

	L	H
adult male carapace	800–900µ	400–500µ
adult female carapace	650–750µ	270–320µ

Ecology: *G. australica* is best known from its type locality, Lake Purrumbete in Victoria. This is a permanent lake with salinity of 0.42–

0.50‰ over the 1969–1972 period (Timms 1976) and 0.37–0.44‰ over 1979–80. It is only recorded in that lake (greatest depth > 40m) at 0.5–1 m by Timms (1973)². It is usually found crawling in among filamentous algae like *G. maia*. In South Australia it is also recorded from Scott Creek near Adelaide, and from the permanent Fresh Dip Lake near Robe. *G. australica* is considered to be a fresh-water species which can withstand a slight amount of dissolved solids in water, with its highest salinity recorded at Fresh Dip Lake at 2.3‰. Brooding occurs in this species as demonstrated by Hussainy (1969). Fossil specimens, with coarse shell reticulation have been recovered with other fresh water ostracods from a short core taken from the fresh Blue Lake at Mt Gambier, S.A.

Remarks: The transfer of this species to *Gomphodella* gen. nov. is necessary because it does not possess the peripheral lateral ridge around the flat base of the shell of each valve so typical of *Gomphocythere* Sars, 1924. This species is easily distinguishable from *G. maia* by its larger size, reticulated shell and the very pointed posterior area of the shell which is also steeply inclined posteroventrally.

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¹ TIMMS, B. V. (1973) A comparative study of the limnology of three maar lakes in western Victoria. Ph.D. Thesis, Monash University (unpubl.).

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THREE NEW SPECIES OF CALOSTAURUS (CESTODA: DAVAINAEIDAE) FROM THE NEW GUINEA WALLABY DORCOPIS VETERUM

BY IAN BEVERIDGE

Summary

Three new species of Calostaurus Sandars (Cestoda: Davaineidae) are described from the small intestine of the macropodid marsupial *Dorcopsis veterum* from New Guinea. *C. dorcopsis* sp. nov. differs from *C. macropus* in the size and arrangement of rostellar spines, size of rostellar hooks and cirrus sac. *C. oweni* sp. nov. and *C. parvus* sp. nov. resemble *C. mundayi* in features of the rostellum, but differ in size, number of testes per proglottis and number of eggs per egg capsule.

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Three new species of *Calostaurus* Sandars (Cestoda: Davainiidae) are described from the small intestine of the macropodid marsupial *Dorcopsis veterum* from New Guinea. *C. dorcopsis* sp. nov. differs from *C. macropus* in the size and arrangement of rostellar spines, size of rostellar hooks and cirrus sac. *C. oweni* sp. nov. and *C. parvus* sp. nov. resemble *C. mundayi* in features of the rostellum, but differ in size, number of testes per proglottis and number of eggs per egg capsule.

Introduction

Three species of the davainiid cestode genus *Calostaurus* Sandars, 1957 are known to occur in Australasian macropodid marsupials, namely *C. macropus* (Ortlepp, 1922) originally described from *Thylogale brunii* (Shreber, 1778) (syn. *Macropus brunii*) and redescribed by Sandars (1957) from *Thylogale stigmatica* Gould, 1860 (syn. *T. wilcoxii*) in Queensland, and *C. thylogale* Beveridge, 1975 and *C. mundayi* from *Thylogale billardieri* (Desmarest, 1822) and *Potorous tridactylus* (Kerr, 1972) (syn. *P. apicalis*) respectively, both occurring in Tasmania (Beveridge, 1975). In each instance, a single host species is parasitised by one cestode species only. By contrast in collections of cestodes made recently from the wallaby *Dorcopsis veterum* (Lesson, 1827) in New Guinea by Dr I. L. Owen, three cestode species may occur in the same host individual. The three species are described in this paper.

Methods

Cestodes were stained with Celestine blue, dehydrated and mounted in balsam. Serial sections of each species were cut but the state of preservation of the specimens did not allow detailed histological examination. All measurements are given in mm as the range followed by the mean of 5 measurements in parentheses.

Calostaurus dorcopsis sp. nov.

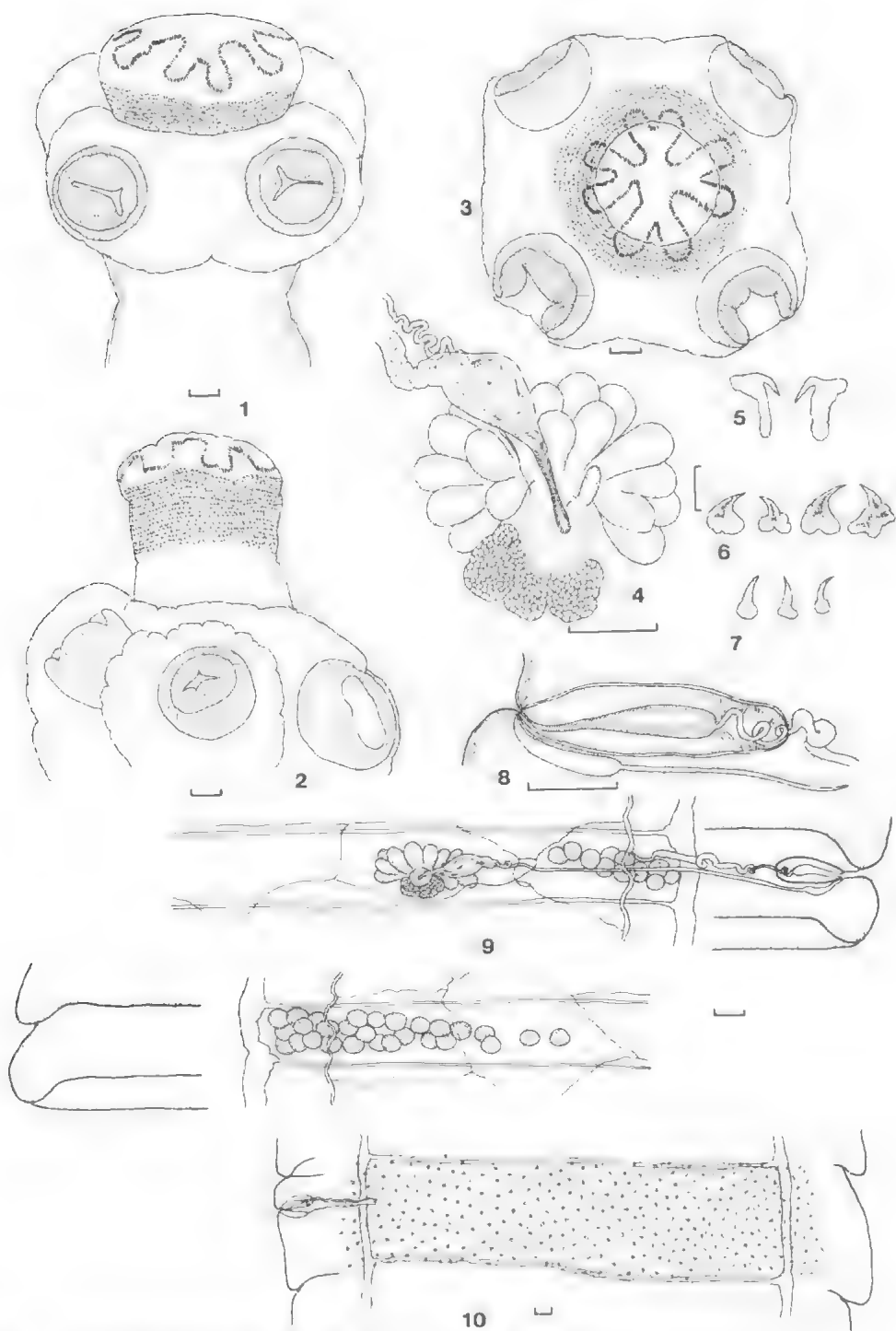
FIGS 1-10

Description based on fragments of several specimens; no complete cestodes present. dorsal system, ramifying across proglottis. In

Moderate sized cestodes. Maximum length of fragments 105; maximum width 4. Largest fragment contains 350 proglottides. Scolex large, 0.90-1.16 (1.00) in diameter, quadrangular in *en face* view, with eversible rostellum 0.42-0.49 (0.52) in diameter. Rostellum armed with approximately 1600 hammer shaped hooks in two rows, arranged in shape of Maltese cross, with axes extending between pairs of suckers; hooks 0.012-0.014 (0.013) long. Base of rostellum armed with approximately 16 transverse rows of rose thorn shaped hooks each 0.007-0.011 (0.010) long, with awl shaped blade and irregular and highly variable bifid base. On everted rostellum, hooks extend almost to extremities of Maltese cross; never lie between arms of cross. Rostellum varies considerably in shape (Figs 1, 2) depending upon degree of extension. Rostellar spines form narrow band anterior to rostellum at opening to rostellar sac when latter fully retracted. Suckers 0.27-0.32 (0.29) in diameter; margins armed with seven to nine rows of tiny awl-shaped spines 0.006-0.008 (0.007) long. Neck 0.38-0.75 (0.52) long.

Proglottides craspedote; velum overhanging adjacent proglottis, very narrow. Mature proglottides greatly extended transversely, 0.20-0.45 (0.36) \times 2.4-4.0 (2.9), ratio width: length 1:5-1:20. Genital pores single, unilateral. Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canal extremely narrow, 0.01-0.03 (0.02) in diameter, lies well internal to ventral canal; ventral osmoregulatory canal 0.05-0.09 (0.07) in diameter. Transverse osmoregulatory canals connect left and right dorsal and ventral canals at posterior margin of each proglottis. Complex, branching network of canals arises from

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Figs 1-10. *Calostaurus dorcopsis* sp. nov. from the wallaby *Dorcopsis veterum*. 1. Scolex with partially everted rostellum. 2. Scolex with fully evert rostellum 3. Scolex with retracted rostellum, *en face* view. 4. Female genitalia, dorsal view. 5. Rostellar hooks. 6. Rostellar spines. 7. Sucker spines. 8. Cirrus sac and distal vagina. 9. Single mature proglottis. 10. Gravid proglottis. Scale lines: Figs 5-7, 0.01 mm; Figs 1-4, 8-10, 0.1 mm.

largest fragment, genital anlage appears in approximately 50th proglottis. Male and female genitalia mature in proglottides 200 and 260 respectively, and involute in proglottides 425 and 340 respectively. First gravid proglottis 345th.

Genital atrium small, situated in anterior half of lateral proglottis margin. Cirrus sac small, 0.20–0.25 (0.22) \times 0.07, elongate, muscular walls feeble, cirrus sac not reaching ventral osmoregulatory canals. Distal region of cirrus of greater internal diameter, lined with bristles; remainder narrow, coiled. Internal and external seminal vesicles absent. Vas deferens slightly coiled, narrow, passes medially towards centre of proglottis, terminating dorsal to ovary. Vasa efferentia not seen. Testes invariably distributed in two lateral groups, extending from ventral osmoregulatory canals, below dorsal canals, medially. Testes densest in lateral regions of each field; testes never overlie female genital glands; testes 0.05–0.06 (0.06) in diameter. Testes number 37–51 per proglottis; always more testes in aporal field; 8–23 (15) testes in poral field, 21–39 (31) in aporal field. Some differences evident in testis number between strobilae: in one strobila 8–13 (10) poral, 34–39 (37) aporal; in second strobila 16–23 (20) poral, 22–28 (24) aporal.

Vagina opens to genital atrium posterior to cirrus sac. Distal region, 0.08–0.13 (0.10) \times 0.02, dilated, armed with fine bristles. Mid-region narrow, uncoiled, leads medially, posterior to vas deferens, terminates in fusiform seminal receptacle 0.12–0.18 (0.15) \times 0.03–0.07 (0.05) in size, lying dorsal to poral lobe of ovary; sperm duct passes posteriorly from seminal receptacle, lined with bristles. Ovary bilobed, situated to poral side of proglottis midline, 0.15–0.20 (0.18) \times 0.26–0.38 (0.32) in size, with 8–10 clavate lobules in each lobe. Vitellarium ovoid or bean-shaped, 0.07–0.09 (0.08) \times 0.12–0.16 (0.15) in size, posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium. Uterine duct short, passes anteriorly from Mehlis' gland, terminates dorsal to ovary. Uterus absent. Eggs discharged from uterine duct directly into parenchyma, become surrounded by capsule, with one egg per egg capsule. Size of egg capsule 0.05–0.06 (0.055); egg 0.01–0.02 (0.015). Gravid proglottides extended transversely 0.21–0.70 (0.49) \times 2.2–3.6 (3.1), width:length ratio 1:3–1:7. Terminal pro-

glottides relatively longer, occasionally as long as wide 0.90–1.10 (1.03) \times 1.05–1.55 (1.31).

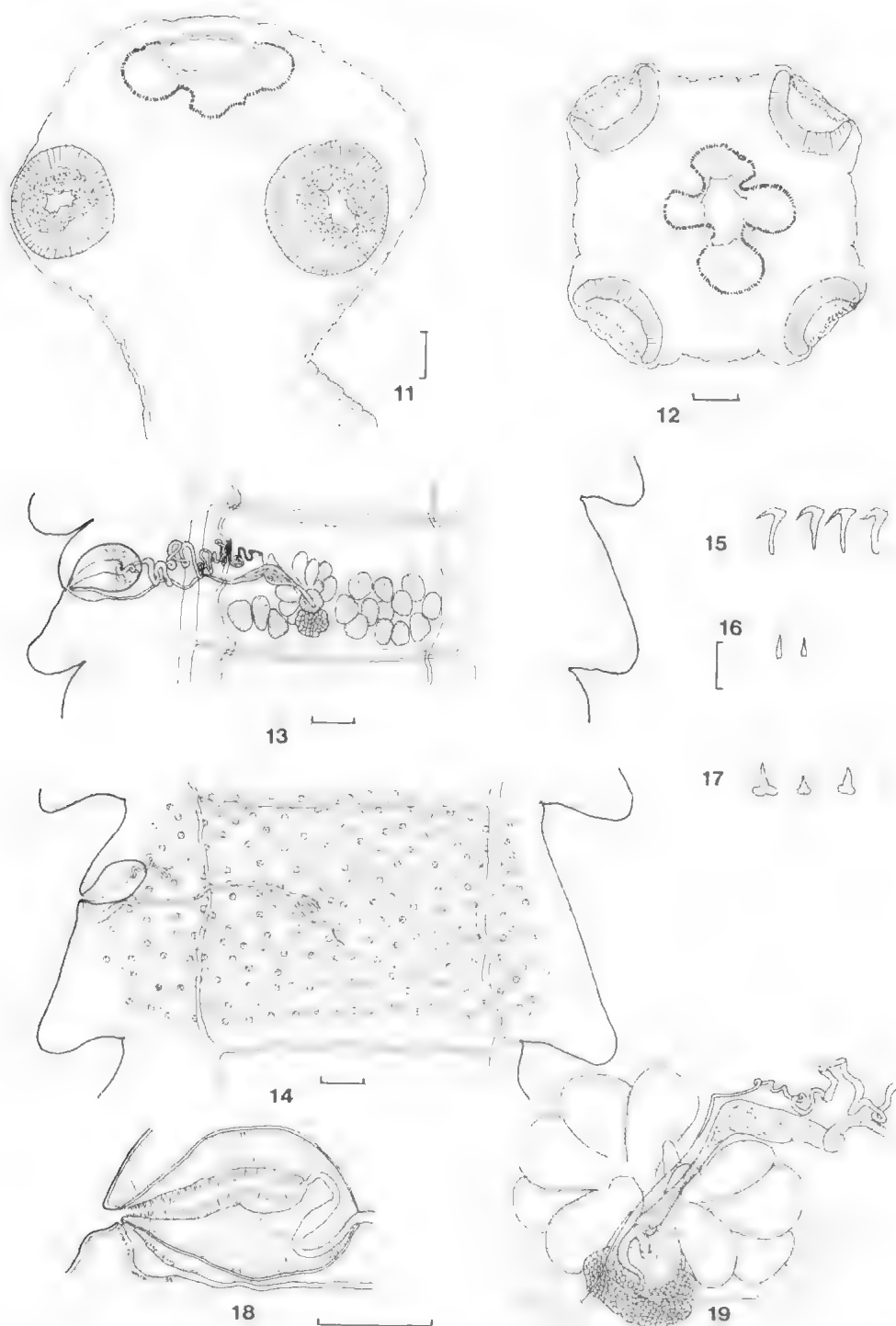
Host: *Dorcopsis veterum* (Lesson, 1827) (Marsupialia: Macropodidae). *Location:* Small intestine. *Type Locality:* Veikabu Creek, Central Province, 9°10'S, 147°09'E, Papua New Guinea. *Types:* In British Museum (Natural History), holotype 1981.6.17.1, paratypes, 1981.6.17.2–10. *Etymology:* The specific name is derived from that of the host.

Calostaurus oweni sp. nov.

FIGS 11–19

Description based on 10 complete mounted specimens. Small cestodes, 24–38 (33) long; maximum width 1.2–1.4 (1.3); strobilae contain 100–147 (120) proglottides. Scolex relatively large, 0.62–1.05 (0.99) in diameter, quadrangular in *en face* view, with rostellum up to 0.45 in diameter when everted. Rostellum armed with approximately 1000 hammer shaped hooks in two rows, arranged in form of open cross, with axes extending between pairs of suckers; rostellar cross 0.25–0.32 (0.29) \times 0.18–0.34 (0.26); rostellar hooks 0.007–0.010 (0.008) long. Base of rostellum armed with concentric rows of tiny awl shaped spines approximately 0.004 long. Spines form band posterior to rostellar cross on everted rostellum, never lie between arms of cross; spines form band anterior to rostellar cross, at opening of rostellar sac when rostellum fully retracted. Suckers 0.16–0.23 (0.21) in diameter; margins armed with about eight rows of tiny, rose thorn shaped spines 0.004–0.007 (0.006) long. Neck 0.21–0.34 (0.28) long.

Proglottides craspedote; velum overhanging adjacent proglottis very narrow. Mature proglottides wider than long, 0.27–0.33 (0.31) \times 1.20–1.33 (1.25), ratio length:width 1:3.5–1:4.3. Genital pores single, unilateral; one proglottis found with reversed orientation. Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canal extremely narrow, 0.005 in diameter, sinuous, lies internal to ventral canal; ventral osmoregulatory canal straight, 0.02–0.04 (0.03) in diameter. Transverse osmoregulatory canals connect left and right dorsal and ventral canals at posterior margin of each proglottis. Origins of dorsal transverse canals sometimes variable, single transverse canal occasionally arising from two or more points on dorsal longitudinal canal.



Figs 11-19. *Calostaurus oweni* sp. nov. from the wallaby *Dorcopsis veterum*. 11. Scolex with retracted rostellum, lateral view. 12. Scolex with retracted rostellum, *en face* view. 13. Mature proglottis. 14. Gravid proglottis. 15. Rostellar hooks. 16. Rostellar spines. 17. Sucker spines. 18. Cirrus sac and distal vagina. 19. Female genitalia dorsal view. Scale lines: Figs 15-17, 0.01 mm; Figs 11-14, 18, 19, 0.1 mm.

Genital anlage appears in proglottides 25–40 (31). Male and female genitalia mature in proglottides 52–73 (64) and 70–98 (81) respectively, and involute in proglottides 85–112 (97) and 75–102 (91) respectively. First gravid proglottis 89–120 (104).

Genital atrium very small, situated in middle of lateral proglottis margin. Cirrus sac large, 0.16–0.18 (0.17) \times 0.09–0.11 (0.10), ovoid, muscular walls feeble, cirrus sac not reaching longitudinal osmoregulatory canals. Distal region of cirrus of greater internal diameter, lined with bristles; remainder narrow, coiled muscle bands run from cirrus to internal surface of cirrus sac. Internal and external seminal vesicles absent. Vas deferens greatly coiled, passes medially towards centre of proglottis, gradually diminishing in diameter, terminates dorsal to ovarian isthmus by dividing into two vasa efferentia each supplying one group of testes. Testes almost invariably distributed in two lateral groups, in posterior half of proglottis, extending medially from dorsal osmoregulatory canals. In very occasional proglottides, one or two testes present posterior to vitellarium joining two lateral testis groups. Testes ovoid, ovarian lobes and occasionally vitellarium; testes 0.045–0.055 (0.050) in diameter. Testes number 15–19 (16) per proglottis; always more testes in aporal field: 3–7 (5) poral, 10–14 (12) aporal.

Vagina opens to genital atrium posterior to cirrus sac. Distal region, 0.05–0.08 (0.07) \times 0.02, dilated. Mid-region narrow, sinuous, leads medially, posterior to vas deferens, terminates in fusiform seminal receptacle, 0.07–0.11 (0.09) \times 0.03–0.04 (0.04) in size, lying anterior and dorsal to poral lobe of ovary; sperm duct passes posteriorly from seminal receptacle, dilates, lined with bristles. Ovary bilobed, situated to poral side of proglottis mid-line, 0.10–0.18 (0.13) \times 0.17–0.20 (0.18) with 4–5 clavate lobules in each lobe. Vitellarium ovoid or bean shaped, lobulate, 0.05–0.07 (0.06) \times 0.07–0.08 (0.07) in size, situated posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium. Uterine duct passes anteriorly from Mehlis' gland terminated in midline dorsal to ovary. Uterus absent. Eggs discharged from uterine duct directly into parenchyma, become surrounded by capsule, with one egg per egg capsule. Size of egg capsule 0.04–0.05 (0.047); egg 0.01–0.02 (0.15). Gravid proglottides extended

transversely 0.41–0.55 (0.45) \times 0.95–1.33 (1.20), width:length ratio 1:1.17–1:2.7. Terminal proglottides almost as long as wide or longer than wide, 0.62–0.75 (0.69) \times 0.52–0.88 (0.70), width:length ratio 1:0.74–1:1.3.

Host: *Dorcopsis veterum* (Lesson, 1827) (Marsupialia: Macropodidae). *Location:* small intestine. *Type Locality:* Veikabu Creek, Central Province, Papua New Guinea. *Types:* In British Museum (Natural History), holotype 1981.6.17.11, paratypes 1981.6.17.12–21.

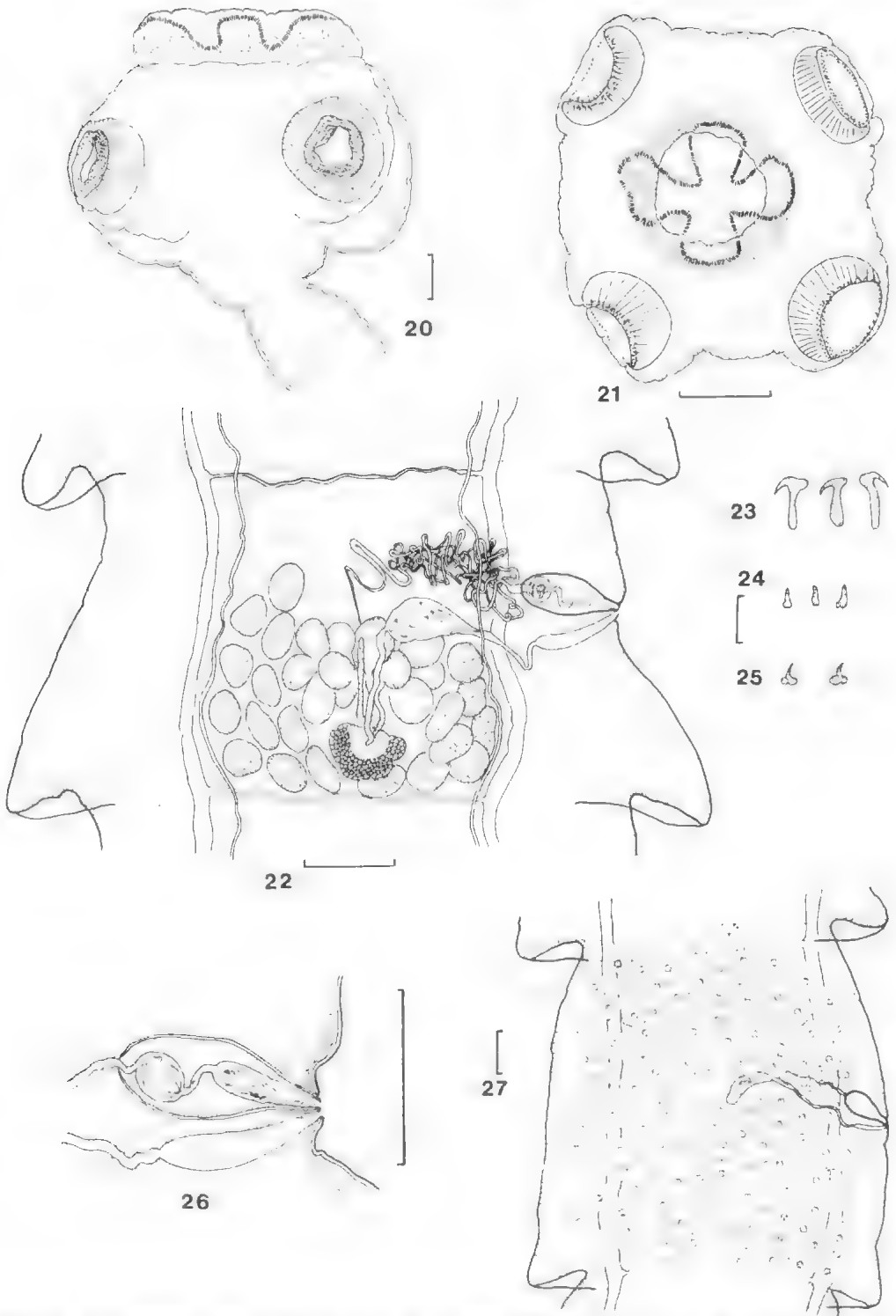
Etymology: this species is named after Dr L. L. Owen who collected all the material described here.

Calostaurus parvus sp. nov.

FIGS 20–27

Description based on five complete mounted specimens. Small cestodes, 9.0–11.2 (9.7) long; maximum width 0.75–1.20 (0.96); strobilae contain 38–57 (42) proglottides. Scolex relatively large, 0.62–1.08 (0.76) in diameter, quadrangular in *en face* view, with eversible rostellum. Rostellum armed with approximately 1000 hammer-shaped hooks in two rows, arranged in form of open cross, with axes extending between pairs of suckers; rostellar cross 0.29–0.47 (0.35) \times 0.28–0.42 (0.34); rostellar hooks 0.009–0.010 (0.010) long. Base of rostellum armed with concentric rows of tiny awl-shaped spines, with simple or bifid base; spines 0.004–0.005 (0.005) long. Spines form band anterior to rostellar cross, at opening of rostellar sac, when rostellum fully retracted. Suckers 0.19–0.23 (0.20) in diameter, margins armed with about 10 rows of tiny rose thorn shaped spines 0.002–0.005 (0.003) long. Neck short.

Proglottides craspedote; velum overhanging adjacent proglottis very narrow. Mature proglottides wider than long 0.24–0.35 (0.32) \times 0.64–0.98 (0.75), ratio length:width 1:2.0–1:3.8. Genital pores single, unilateral. Genital ducts pass between longitudinal osmoregulatory canals. Dorsal osmoregulatory canal extremely narrow, sinuous, 0.005–0.010 (0.006) in diameter, lies immediately internal to ventral canal; ventral osmoregulatory canal 0.015–0.020 (0.017) in diameter. Transverse osmoregulatory canals connect left and right ventral canals at posterior margin of each proglottis. Genital anlage appears in proglottides 8–28 (12). Male and female genitalia mature in



Figs 20-27. *Calostaurus parvus* sp. nov. from the wallaby *Dorcopsis veterum*. 20. Scolex with everted rostellum, lateral view. 21. Scolex with retracted rostellum, en face view. 22. Mature proglottis. 23. Rostellar hooks. 24. Rostellar spines. 25. Sucker spines. 26. Cirrus sac and distal vagina. 27. Gravid proglottis. Scale lines: Figs 23-25, 0.01 mm; Figs 20-22, 26, 27, 0.1 mm.

proglottides 14–37 (22) and 20–28 (25) respectively and involute in proglottides 33–36 (35) and 30–34 (32) respectively. First gravid proglottis 34–38 (36).

Genital atrium insignificant, situated slightly anterior to middle of lateral proglottis margin. Cirrus sac small, 0.07–0.10 (0.09) \times 0.04–0.05 (0.04), clavate, muscular walls feeble, cirrus sac almost reaching longitudinal osmoregulatory canals. Distal region of cirrus of greater internal diameter; armature not seen; mid-region narrow, sinuous; proximal region forms small, spherical internal seminal vesicle; present in most proglottides of all strobilae examined, but not detectable in every single proglottis; internal seminal vesicle 0.020–0.035 (0.025) \times 0.025–0.030 (0.026). External seminal vesicle absent. Vas deferens narrow, greatly coiled, surrounded by pale basophilic cells, passes medially towards centre of proglottis, then posteriorly towards ovary; terminates dorsal to ovarian isthmus; vasa efferentia not seen. Testes distributed in posterior part of proglottis, in single field, confluent posterior to vitellarium; testes lie within area bounded by lateral osmoregulatory canals; usually lie medial to dorsal canals, but few testes may overlie dorsal canals. Testes not confluent posterior to vitellaria in few proglottides. Testes usually overlie ovary and vitellarium; testes 0.04–0.05 (0.045) in diameter. Testes number 17–22 (20) per proglottis; paratestes 6–10 (8), invariably less numerous than aporal testes 11–14 (13).

Vagina opens to genital atrium posterior to cirrus sac. Distal region, 0.06 \times 0.02, dilated. Mid-region narrow, sinuous, leads medially, posterior to vas deferens, terminating in large clavate to pyriform seminal receptacle, 0.08–0.13 (0.09) \times 0.04–0.05 (0.05), lying anterior and dorsal to paratestes of ovary; sperm duct elongate, sinuous, passes posteriorly from seminal receptacle. Ovary bilobed, situated in proglottis mid-line, 0.09–0.16 (0.14) \times 0.14–0.16 (0.15) in size with 4–6 clavate lobules in each lobe. Vitellarium ovoid or bean shaped, lobulate, 0.05–0.08 (0.06) \times 0.04–0.05 (0.05) in size, situated posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium. Uterine duct passes anteriorly from Mehlis' gland, terminates in midline, anterior to ovary. Uterus absent. Eggs discharged from uterine duct directly into parenchyma, become surrounded by capsules, with one egg per egg capsule. Size

of egg capsule 0.05–0.07 (0.06); egg 0.015. Gravid proglottides longer than wide 0.65–0.75 (0.69) \times 0.67–1.10 (0.83), ratio length:width 0.64:1–1:1.1. Terminal proglottides 0.85 \times 0.58–0.68 (0.73), ratio length:width 1.2:1–1.4:1.

Host: *Dorcopsis veterum* (Lesson, 1827) (Marsupialia: Macropodidae). *Location:* Small intestine. *Type locality:* Veikabu Creek, Central Province, Papua New Guinea. *Types:* In British Museum (Natural History), holotype 1981.6.19.1, paratypes 1981.6.19.2–6. *Etymology:* the specific name *parvus* derives from the fact that it is the smallest known species of the genus.

Discussion

Three species of *Calostaurus* have been described previously, being distinguished principally by the shape of the cross formed by the rostellar hooks. *C. macropus* has the hooks arranged in the shape of a Maltese cross, *C. thylogale* in a six-lobed circle and *C. mundayi* in a four-lobed cross. Of the species described here, *C. dorcopsis* sp. nov., most closely resembles *C. macropus* in that the hooks are arranged in the form of a Maltese cross whereas *C. oweni* sp. nov. and *C. parvus* sp. nov. both have rostellar hooks arranged in the form of four-lobed crosses similar to that of *C. mundayi*. The histological anatomy of the scoleces of the new species is similar to that of *C. thylogale* and *C. mundayi* and has therefore not been described in detail.

Both *C. oweni* and *C. parvus* can be distinguished from *C. mundayi* by size alone, since *C. mundayi* measures 32.4 to 45.1 cm, whereas *C. oweni* and *C. parvus* measure 2.4–3.8 and 0.9–1.1 cm respectively. In addition *C. mundayi* has one to three eggs per egg capsule while the other species have a single egg in each capsule, and the range of testis number in *C. mundayi* (25–32) is higher than in *C. oweni* (15–19) and *C. parvus* (17–22).

C. oweni and *C. parvus* differ from one another in a number of features. Gravid specimens of *C. parvus* are consistently smaller and have fewer proglottides than *C. oweni*, and there is a difference in the rate of development and involution of the genital organs in the two species. The testes are generally confluent posterior to the vitellaria in *C. parvus*, but are divided into two groups in *C. oweni*. Some variation in this character does occur and

TABLE 1. Principal features and measurements of species of *Calostaurus*

Species	Length (cm)	No. proglottides	Form of cross	Length of rostellar hooks (μ m)	No. rostellar hooks	Size of cirrus sac (mm)	Internal seminal vesicle	No. testes per proglottis p = poral ap = aporal	Testes extend beyond dorsal osmoregulatory canals	Testes confluent posterior to vitellarium	No. eggs per Capsule
<i>C. macropus</i> Ortlepp (1922)	24-35	—	Maltese cross	9	1300	0.10	—	50	— (from type)	—	1
Sandars (1957)	4-5	—	Maltese cross	—	2500	0.08-0.12	—	35-55 p 12-16 ap 22-29	— (from new specs)	—	1
<i>C. thylogale</i>	34.5	hundreds	6 lobed circle	30-40	300-350	0.10-0.14	—	70-94 p 26-26 ap 50-73	—	+	1
<i>C. mundayi</i>	32.4-45.1	hundreds	4 lobed cross	10-13	700	0.10-0.11	—	25-32 p 5-11 ap 16-22	—	—	1-3 (2)
<i>C. dorcopsis</i>	>10.5	>350	Maltese cross	12-15	1600	0.20-0.25	—	37-51 p 8-23 ap 21-39	+	—	1
<i>C. oweni</i>	2.4-3.8	100-147	4 lobed cross	7-10	1000	0.16-0.18	—	15-19 p 3-7 ap 10-14	—	—	1
<i>C. parvus</i>	0.9-1.1	38-57	4 lobed cross	9-10	1000	0.07-0.10	+	17-22 p 6-10 ap 11-14	—	+	1

occasional proglottides of *C. parvus* have the testes in two groups, while occasional proglottides of *C. oweni* have the testes confluent posterior to the vitellaria, but in an individual strobila, one form or the other very clearly predominates. The cirrus sac of *C. parvus* (0.07–0.010 mm) is invariably smaller than that of *C. oweni* (0.16–0.18) though the size difference may be a reflection of overall cestode size. However, all specimens of *C. parvus* examined possess an internal seminal vesicle, a feature which is not present in any congener. It is not detectable in every single proglottis, but is invariably visible in some proglottides of a strobila. These various differences are considered adequate for the erection of two new species.

Comparisons of *C. dorcopsis* with *C. macropus* are complicated by the fact that the latter species has been described on two occasions firstly by Ortlepp (1922) from *Thylogale brunii* and later by Sandars (1957) from *Thylogale stigmatica* (= *Thylogale wilcoxii*), the descriptions differing on some important features such as size and the number of the rostellar hooks.

C. dorcopsis is similar to both descriptions of *C. macropus* in the form of the rostellar cross, in the number and distribution of the testes and in the transversely elongated mature proglottis. *C. dorcopsis* would appear to differ from all congeners by the distribution of the testes which extend laterally beyond the dorsal osmoregulatory canals to the medial edge of the ventral canals. However, this condition also exists in the type material of *C. macropus* in the British Museum (Natural History), (though not stated by Ortlepp (1922) in his description) and in material collected by me from *Thylogale stigmatica* in Queensland, conforming in all respects to the specimens described by Sandars (1957) from the same host and same general geographic region. Sandars (1957) gave the locality of her specimens incorrectly as 'Mt. Tamborine in South Australia'; Mt. Tamborine is in Queensland; no species of *Thylogale* occur in South Australia.

C. dorcopsis differs from *C. macropus* in a number of features. The cirrus sac in *C. dorcopsis* (0.20–0.25) mm) is larger than in descriptions of *C. macropus* (0.10, 0.08–0.12 mm); the rostellar hooks of *C. dorcopsis* (12–15 µm) are slightly longer than those of

C. macropus (9 µm) and the rostellar spines of *C. dorcopsis* (7–11 µm) are longer than those of *C. macropus* (5–6 µm) and are of a different shape. The differences in the rostellar spines are very striking indeed as they are very prominent rose-thorn structures on the rostellum of *C. dorcopsis* but are inconspicuous and awl or hook shaped on rostellum of *C. macropus*. Both Ortlepp (1922) and Sandars (1957) described and illustrated the rostellar spines of *C. macropus* as covering the entire rostellum with the exception of the area inside the rostellar cross. It has not been possible to verify this situation since in the type specimen examined by me and in the new material from *T. stigmatica*, most of the rostellar spines are missing. Assuming the earlier descriptions to be correct, *C. dorcopsis* differs markedly from *C. macropus* in having the rostellar spines arranged in about 20 transverse rows, forming a distinct band on the everted rostellum but never covering the entire surface of it.

Because of these differences, *C. dorcopsis* sp. nov. has been described. It is evident however that the morphology of *C. macropus* requires re-investigation based on new material from the type host, *T. brunii*. The extant type material is inadequate for a thorough re-description and the status of specimens from *T. stigmatica*, described by Sandars (1957) as *C. macropus* requires clarification.

The principal differences between species of *Calostaurus* are shown in Table 1.

Acknowledgements

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FROG FAUNA OF THE NORTHERN TERRITORY: NEW DISTRIBUTIONAL RECORDS AND THE DESCRIPTION OF A NEW SPECIES

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TYLER, M. J., DAVIES, M. & MARTIN, A. A. (1981) Frog fauna of the Northern Territory: new distributional records and the description of a new species, *Trans. R. Soc. S. Aust.* **105** (3), 149-154, 11 December, 1981.

Uperoleia trachyderma sp. nov. is described from the Northern Territory, and additional biological and distributional data are given on *U. lithomoda* Tyler, Davies & Martin. *Rani-della deserticola* Liem & Ingram is recorded in the Northern Territory for the first time, and *Cyclorana cryptotis* Tyler & Martin is recorded for the second time.

Introduction

Our collaborative studies on the frogs of northern Australia have led to the addition of seven species to the North Territory fauna (Martin, *et al.* 1980; Tyler, *et al.* 1978, 1981a; Tyler, *et al.* 1979). Our previous field studies in the Northern Territory have been confined to the East Alligator River area.

However in December 1980 we collected at various sites on the Stuart Highway between Darwin and Tennant Creek. These collections include a new species of the leptodaetylid genus *Uperoleia*, and a second leptodaetylid species not previously recorded from the Northern Territory. We also provide additional information on the distribution and biology of *U. lithomoda* Tyler, Davies & Martin, previously recorded in the N.T. only from the flood plains west of Arnhem Land (Tyler *et al.* 1981a), and the hylid *Cyclorana cryptotis* Tyler & Martin.

Material and Methods

The specimens reported here are located in the following collections: American Museum of Natural History (AMNH); Northern Territory Museum, Darwin (NTM); Museum of Natural History, University of Kansas, Lawrence (KU); South Australian Museum (SAM).

Methods of measurement follow Tyler (1968). Abbreviations used in the text are: E (eye diameter), E-N (eye to naris distance), IN (internarial span), S-V (snout to vent length), TL (tibia length).

Osteological data were obtained from cleared and Alizarin Red stained preparations using the technique of Davis & Gore (1947). Osteological descriptions follow Trueb (1979).

Male mating calls were recorded with a Sony TC-510-2 tape recorder and a Beyer M 88 dynamic microphone, at a tape speed of 19 cm/sec. Wet-bulb air temperatures were measured close to the calling sites of males using a Schultheis quick-reading thermometer. Calls were analysed by means of a UV oscillograph (San-Ei Visilight) and a sound spectrograph (Kay Model 6061-B Sona-Graph) with the overall response curve maintained in the FL-1 position. Three calls of each male were analysed and mean values calculated.

FAMILY: Leptodaetylidae

Uperoleia trachyderma sp. nov.

FIGS 1-4

Holotype. SAM R20374, an adult male collected on the Newcastle Creek floodplain at the George Redman Causeway (17°14'S; 133°28'E) 37 km N of Elliot, N.T. on 16.xii.80 by M. Davies, A. A. Martin and M. J. Tyler.

Definition: A small species (males 20.3-22.0 mm S-V) with small eyes (eye diameter equivalent to eye to naris distance), with the dorsum covered with small, conical tubercles, and with a heavily pigmented ventral surface. Mating call a staccato burst of four short pulses.

Description of holotype: Maxillary and vomerine teeth absent. Snout elongate, pointed when viewed from above; projecting slightly in profile. Eye to naris distance greater than internarial span (E-N/IN 1.27). Canthus rostralis straight. Tympanum not visible externally (Fig. 1).

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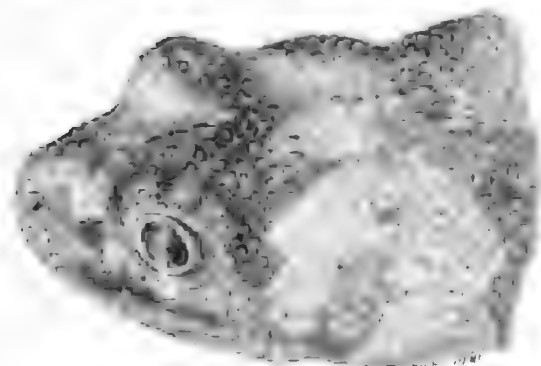


Fig. 1. Dorsolateral view of head of *Uperoleia pachyderma*.

Fingers long, slender, unwebbed and unfringed with prominent subarticular tubercles and well developed palmar tubercles (Fig. 2A). Fingers in order of length $3 > 4 > 2 > 1$. Hindlimbs very short (TL/S-V 0.35). Toes long, slender, slightly fringed and unwebbed (Fig. 2B). Toes in order of length $4 > 3 > 5 > 2 > 1$. Metatarsal tubercles small and poorly developed. Subarticular tubercles small but prominent.

Dorsal surface densely covered with small, conical tubercles. Parotoid and inguinal glands inconspicuous; coccygeal glands not visible externally. Ventral surface finely granular. Cloacal flap narrow but well developed. No heel tubercles.

Dorsal surface dull slate with obscure, slightly darker mottling; glands faintly creamish. Inguinal and post-femoral flash markings dull red. On ventral surface sub-mandibular area pale grey; abdomen with numerous small islands of pale grey on a white background.

Dimensions: Snout to vent length 20.75 mm; tibia length 7.3 mm; eye to naris distance 1.9 mm; internarial span 1.5 mm; eye diameter 1.9 mm.

Variation: There are four paratypes; all are adult males: KU 189561, NTM 9865, SAM R20375-6. The series was collected with the holotype.

The range of body size spans only 1.7 mm (20.3-22.0 mm S-V). The hindlimbs are short (TL/S-V 0.33-0.36) and the metatarsal tubercles (so well developed in congeners) are comparatively poorly developed. The eye diameter is consistently small and approximates the eye to naris distance. The eye to naris dis-

tance is greater than the internarial span (E-N/IN 1.13-1.40).

The unusual tubercular condition of the dorsal skin is apparent in all specimens, and in some is more conspicuous than in the holotype.

The dorsal coloration is reasonably uniform except that in one specimen the parotoid, inguinal and coccygeal glands are bright yellow-cream and stippled with black. In all specimens the dark mottling on the abdomen is more conspicuous than in the holotype.

In life the dorsum is variegated with clearly defined patches of grey on a paler grey ground colour, except for the dermal glands which are suffused with pale orange. The inguinal and post-femoral flash markings are bright carmine. The sub-mandibular area is slate, and the abdomen is marked with islands of grey upon a creamish-grey background.

Osteology: Skull (Fig. 3A) moderately ossified, sloping anteroventrally. Sphenethmoid poorly ossified, not conjoined medially either dorsally or ventrally. Dorsally sphenethmoid in tenuous contact with nasals. Ossified portion of sphenethmoid extending ventrally for about $\frac{1}{3}$ length of orbit. Prootic and exoccipital not fused dorso- or ventromedially. Fenestrae present dorsally and ventrally in crista parotica. Crista parotica short, thick, slightly overlapped medially by posterior extremities of frontoparietals, widely separated laterally from unexpanded otic rami of squamosals.

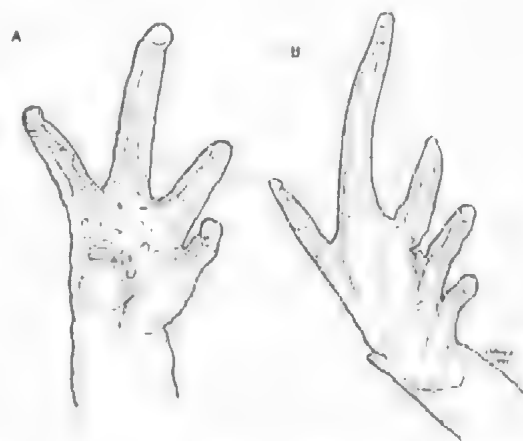


Fig. 2. (A) Palmar view of hand and (B) plantar view of foot of *Uperoleia pachyderma*.

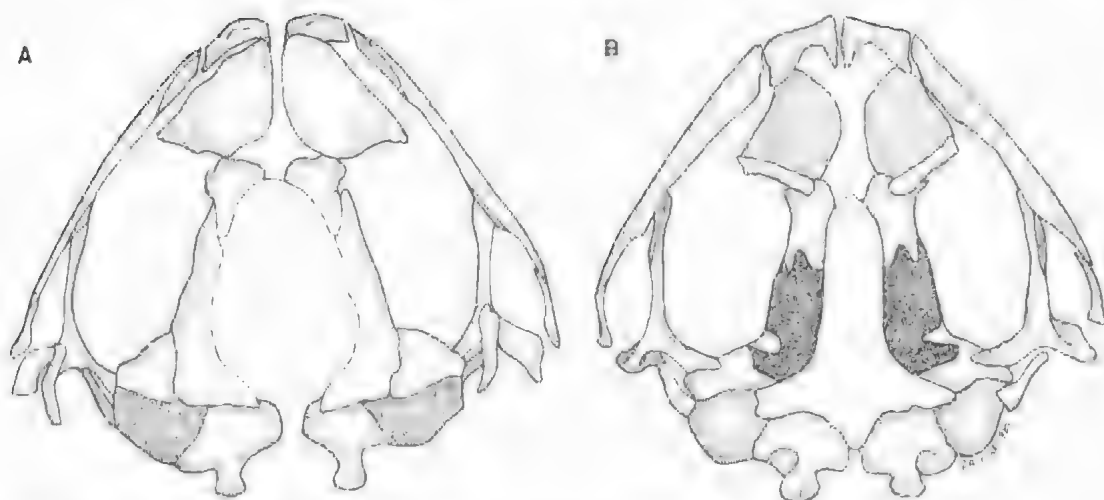


Fig. 3. (A) Dorsal and (B) ventral view of skull of *Uperoleia trachyderma*.

Frontoparietal fontanelle extensively exposed; anterior and posterior extremities being undefined because of lack of medial ossification of sphenethmoid and exoccipital regions. Nasals extremely well ossified, lying alongside each other medially. Maxillary processes of nasals short and acuminate, not in bony contact with very poorly developed preorbital process of shallow pars facialis of maxillary.

Palatines reduced (Fig. 3B), moderately broad, overlying ossified portion of sphenethmoid medially at angle of approx. 45° .

Parasphenoid robust; long, broad cultriform process, almost truncate, reaching to level of posterior edge of palatines. Alae broad, short, slightly angled posteriorly from cultriform process. Pterygoids moderately robust; anterior arm slender, in moderately short contact with poorly developed pterygoid process of palatal shelf of maxillary. Medial arm moderately long, very robust; posterior arm short and moderately sharp.

Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosals stocky, no zygomatic ramus, long unexpanded otic ramus. Maxillary and premaxillary edentate. Alary processes of premaxillaries moderately broad, perpendicular to premaxillary. Palatine processes of premaxillaries well developed, not abutting medially. Palatal shelf moderately deep with poorly developed pterygoid process. Prevomers absent. Bony columella present.

Pectoral girdle arciferal, robust. Omosternum absent, xiphisternum present. Clavicles slender, curved, closely applied medially. Coracoids robust, widely separated medially. Bicapitate scapula considerably shorter than clavicles. Suprascapula about $\frac{1}{2}$ ossified.

Eight procoelous non-imbricate presacral vertebrae. Sacral diapophyses poorly to moderately expanded. Relative widths of transverse processes $\text{III} > \text{sacrum} > \text{IV} > \text{II} > \text{V} = \text{VI} = \text{VII} = \text{VIII}$. Iliia extending to anterior extremity of sacral diapophyses. Sacrocoelocyeal articulation bicondylar. Urostyle with well developed crest extending about $\frac{1}{4}$ of its length.

Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2-2-3-3. No bony prepollex. Palmar sesamoids present. Phalangeal formula of foot 2-2-3-4-3. Well developed bony prehallux. Terminal phalanges knobbed.

Comparison with other species: *Uperoleia trachyderma* is a distinctive species, particularly in the dorsal skin texture of dense, small but prominent tubercles. Other species with extensive frontoparietal fontanelles comparable to the condition in *U. trachyderma* (*U. russelli*, *U. arenicola*, *U. borealis*, *U. talpa*, and *U. orientalis*) have moderate to extensive webbing between the toes (except in *U. arenicola*). *Uperoleia arenicola* resembles *U. trachyderma* in lacking webbing, but the dorsal skin is smooth or weakly tubercular (tubercular in *U. trachyderma*). The call of *U. orientalis*

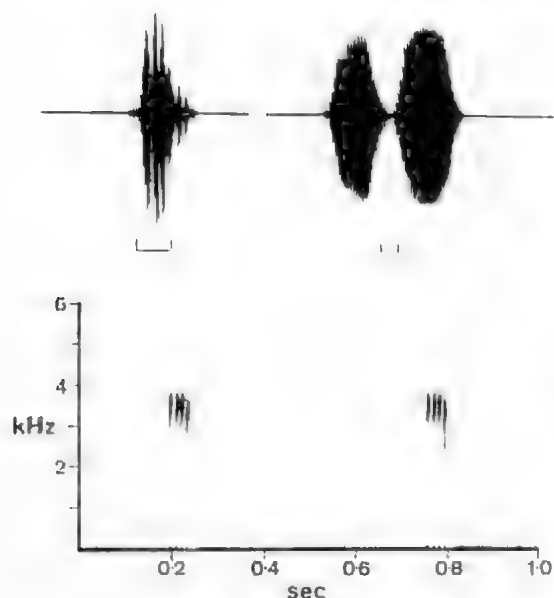


Fig. 4. Upper: oscillographic tracings of male mating calls of: left, *Uperoleia lithomoda*, 6.4 km N of Katherine, N.T.; right, *Ranidella deserticola*, 40 km N of Elliot, N.T. The time marker in each case is 10 msec. Lower: audio-spectrogram (300 Hz bandpass) of two consecutive calls of *Uperoleia trachyderma*, 37 km N of Elliott, N.T.

(which has moderate toe webbing) is not known, but it is probably a larger species (males 26–28 mm, compared with 20–22 mm in the small sample of *U. trachyderma*). No other northwestern Australian congener is known to have a four-pulsed mating call.

The similar-sized *U. lithomoda* taken north of the site of *U. trachyderma* has poorly developed dorsal tubercles, a shorter call, a very poorly exposed frontoparietal foramen, and larger eyes.

Mating call: Calls of two males were recorded 37 km N of Elliot, N.T., on 16.xii.80. An audiospectrogram of a call is shown in Fig. 4, and physical characteristics of calls are listed in Table 1. The call is a harsh "creak", consisting of four short pulses produced in about 50 msec. The pulse repetition rate is about 79 pulses/sec and the dominant frequency about 3600 Hz.

Distribution: Known only from the type locality.

Habitat: The type locality is a flat floodplain of adhesive yellow clay. Males were calling from the base of grass tussocks growing in the water. The surroundings were flooded to a depth of 0.3 m.

Etymology: From the Greek *trachys*, 'rough', and *derma* 'skin', in reference to the unusual skin condition.

Ranidella deserticola Liem & Ingram, 1977

This species was known previously from localities in southwestern Queensland (Liem & Ingram 1977, Tyler 1978) and northeastern South Australia (Brooks 1980).

We found *R. deserticola* upon the Newcastle Creek floodplain 40 km north of Elliot (170°14'S; 133°28'E) on 16.xii.80. Five males and one female were collected beneath debris at the edge of a deep dam (SAM R19118–23). Calls of two males were recorded at a wet bulb air temperature of 25.4°C.

An oscillographic tracing of a call is shown in Fig. 4. Call structure is similar to that described by Liem & Ingram (1977), but two clear emphasized frequency bands are evident

TABLE 1. Physical characteristics of male mating calls of *Uperoleia trachyderma* and *U. lithomoda*. Mean values are given with ranges in parentheses.

Species and locality	N	No. of pulses	Duration (msec)	Pulse repetition rate (pulses/sec)	Dominant frequency (Hz)	Wet bulb temp. (°C)
<i>U. trachyderma</i> 37 km N of Elliot, N.T.	2	4 (4)	51.4 (48.0–54.7)	78.5 (73.0–84.0)	3600 (3500–3700)	24.2–27.0
<i>U. lithomoda</i> 6.4 km N of Katherine, N.T.	3	5.3 (5–6)	16.3 (13.0–20.0)	342 (250–462)	3250 (3150–3400)	26.5
<i>U. lithomoda</i> 11.5 km N of Lake Argyle Village, W.A.	5	4.6 (4–5)	11.6 (9.0–13.0)	401 (333–456)	3420 (3200–3600)	26.0

at about 3450 and 4050 Hz. The note duration and call duration are shorter than recorded by Liem & Ingram (1977), but their recording may have been made at a lower temperature; they gave no temperature data. Values from our recordings are: call duration, 79-80 msec; first note duration, 24-32 msec; second note duration, 33-41 msec.

Examination of other collections reveals that *R. deserticola* is abundant in the Newcastle Waters area. M. Gillam found specimens (SAM R19184) 24 km W of Newcastle Waters homestead (17°32'S, 133°22'E) on 1.xi.76 in hollows on the mud banks of a turkey nest dam. G. A. Crook and W. Zeidler collected 16 specimens at Lake Woods, 15 km WNW of Elliot on 5.x.77 (SAM R19137-52). P. Spalding and W. Hosmer collected the species at Elliot on 11.iv.60 (AMNH 67143-45), Newcastle Waters on 13.iv.60 (AMNH 67146-52) and Anthony Lagoon on 23.iv.60 (AMNH 67153).

Snout to vent lengths of our series and those found by Crook and Zeidler are: males 14.6-18.7 mm; females 14.6-17.8 mm. Liem & Ingram (1977) cite a range of 13.0-18.4 mm for their series, but do not indicate the sex of the specimens. Presumably it embraces the range of both sexes.

The only congeners recorded from Northern Territory are *R. bilineata* Martin, Tyler & Davies (1980) and *R. remota* Tyler & Parker. From the former *R. deserticola* can be distinguished by its smaller size (*bilineata* males 15.5-23.3 mm; females 17.4-20.0 mm S-V) and different mating call. We located *R. bilineata* calling within 10 km of Katherine Gorge. Most of the Northern Territory records of *remota* by Barker & Grigg (1977) and Cogger (1979) are presumably based on *bilineata*. However *remota* occurs in Queensland and it might occupy the eastern portion of Northern Territory. It is distinguished most readily by its long, highly pulsed call (Tyler & Parker 1974).

Uperoleia lithomoda Tyler, Davies & Martin, 1981

Uperoleia lithomoda was known previously from two disjunct populations: one in the eastern Kimberley region, W.A., and one on the flood plains west of Arnhem Land, N.T. (Tyler *et al.* 1981a). We have now partially

closed the intervening gap by obtaining specimens of *U. lithomoda* near Katherine, N.T.

On 14.xii.80 we collected seven adult males and one adult female (SAM R20440-7) of this species within 5 m of the Stuart Highway 6.4 km N of Katherine (1.4 km N of the northern limit of Katherine township) (14°25'S; 132°16'E), and recorded the calls of three males. Snout-vent length of the males ranges 19.9-22.4 mm, and of the female is 22.1 mm. The female is gravid, containing pigmented ovarian eggs 1.2 mm in diameter.

In most respects the morphology of these individuals is similar to that of other populations. However in life the dermal glands are light golden, appearing as continuous stripes along the sides. The flash markings in the groin and behind the thighs are scarlet.

To the ear the mating call is a single, abrupt "click"; and in fact Tyler *et al.* (1981a) described the call of the Kimberley population as consisting of a single pulse. However oscillographic analysis of the calls of Katherine males showed the call to consist of a rapid burst of pulses. Hence calls of the Kimberley populations were re-analysed, and also shown to have multiple-pulsed calls. Fig. 4 shows an oscillographic tracing of the call of a Katherine male; and Table 1 lists the physical characteristics of calls of Kimberley and Katherine males.

The call of *U. lithomoda* may be described as a short burst of 4-6 pulses in 9-20 msec, with a pulse repetition rate of 250-450 pulses/sec. The dominant frequency is about 3300 Hz.

FAMILY: Hylidae

Cyclorana cryptotis Tyler & Martin, 1975

This species was described from an adult male collected at Daly Waters on 13.xii.1971; we found a further single adult male upon the George Redman Causeway, 37 km N of Elliot on 16.xii.1980. Our specimen (SAM R18973) was amongst a large number of *C. cultripes* Parker active on the road surface. (We collected 41 in 15 mins; many more individuals were present, whilst *C. australis* and *C. maculosis* were present but slightly less abundant).

In the Kimberley of W.A. *C. cryptotis* breeds in February, and *C. cultripes* is encountered rarely in that period (Tyler *et al.* 1981b, 1982). Our experiences with these

species permit the interpretation that in the N.T. *C. cryptotis* and *C. culripes* have a similar breeding sequence.

The additional record extends the known range of *C. cryptotis* in the N.T. 110 km further south. We note that *C. cryptotis* is absent from the northern floodplain of the N.T., and the species occupies a narrow latitudinal zone illustrated by Tyler *et al.* (1982).

Acknowledgements

We are grateful to the Australian Research Grants Committee for the grant to M. J. Tyler funding our field study, and to the

Northern Territory Conservation Commission for issuing licence SL54/80, permitting us to undertake the research. Dr R. G. Zweifel provided access to M. J. T. to examine specimens in the collection of the American Museum of Natural History.

We wish to express our gratitude to Mr G. Mewett, formerly of Ansett Airlines for assistance with transfer of freight, Mr C. Miller for expert laboratory assistance, and Mr P. Kempster for numerous photographic prints. Call analyses were carried out by Mr P. A. Harrison, and the manuscript was typed by Mrs J. Russell-Price.

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NEW RECORDS OF OPHIUROIDEA (ECHINODERMATA) FROM SOUTHERN AUSTRALIA, INCLUDING NEW SPECIES OF OPHIACANTHA AND OPHIONEREIS

BY ALAN N. BAKER & DENNIS M. DEVANEY

Summary

Twenty-three ophiuroid species are discussed: nine are new to the region, and the known range of a further seven is extended. *Ophionereis terba* n. sp. and *Ophiacantha shaepherdi* n. sp., are described from Victorian and South Australian waters respectively, and a key to the southern Australian species of *Ophiacantha* is provided. *Ophioceres bispinosus*, *Ophioconis opacum*, and *Ophioprium rosea* are new combinations, and the following species are synonymised: *Ophiacantha abyssicola otagoensis* Fell with *O. brachygnatha* H. L. Clark, *Ophiacantha truncata* Koehler with *Ophioprium rosea* (Lyman), and *Ophiactis laevis* H. L. Clark with *O. tricolor* H. L. Clark. Illustrations are given of holotypes of *Ophioceres bisponus*, *Ophiomusium anisacanthum*, *O. australe*, *Ophionereis lineata*, *Amphiura trisacantha*, *Ophriothrix* (*Placophiothrix*) *albostrata*, *O. Placophiothrix*) *lineocerulea*, and *O. (Keystonea) hymenacantha*. A lectotype is designated for *Ophiocantha clavigera* Koehler.

NEW RECORDS OF OPHIUROIDEA (ECHINODERMATA) FROM SOUTHERN AUSTRALIA, INCLUDING NEW SPECIES OF OPHIACANTHA AND OPHIONEREIS

by ALAN N. BAKER* & DENNIS M. DEVANEY†

Summary

BAKER, A. N. & DEVANEY, D. M. (1981). New records of Ophiuroidea (Echinodermata) from southern Australia, including new species of *Ophiacantha* and *Ophionereis*. *Trans. R. Soc. S. Aust.* **105**(4), 155-178, 11 December, 1981.

Twenty-three ophiuroid species are discussed: nine are new to the region, and the known range of a further seven is extended. *Ophionereis terba* n. sp. and *Ophiacantha shepherd* n. sp., are described from Victorian and South Australian waters respectively, and a key to the southern Australian species of *Ophiacantha* is provided. *Ophioceres bispinosus*, *Ophiocentis opacum*, and *Ophioprium rosea* are new combinations, and the following species are synonymised: *Ophiacantha abyssicola otagoensis* Fell with *O. brachygnatha* H. L. Clark, *Ophiacantha truncata* Koshler with *Ophioprium rosea* (Lyman), and *Ophiactis laevis* H. L. Clark with *O. tricolor* H. L. Clark. Illustrations are given of holotypes of *Ophioceres bispinosus*, *Ophiomusium amisacanthum*, *O. australe*, *Ophionereis lineata*, *Amphipura trisacantha*, *Ophiorhix* (*Placophiorhix*) *albostrigata*, *O. (Placophiorhix) lineocaverrulea*, and *O. (Keystonea) hymenacantha*. A lectotype is designated for *Ophiacantha clavigera* Koshler.

Introduction

The ophiuroid fauna of southern Australian waters is known largely from the studies of H. L. Clark (1916, 1918, 1928, 1938, 1946) and A. M. Clark (1966). H. L. Clark's early paper covered collections trawled from the continental shelf by F.I.S. "Endeavour" in 1910-14, and the later works dealt with specimens collected mainly from the Victorian coast by Joseph Gabriel, and from South Australian waters by Sir Joseph Verco and Clark himself during a visit in 1929. In 1946, Clark added more specimens in his revision of the entire Australian echinoderm fauna. The recent account by A. M. Clark was based on shallow water collections made during the Port Phillip Survey, Victoria, 1957-63. The collections reported by these authors are in the South Australian Museum, National Museum of Victoria, Australian Museum, Museum of Comparative Zoology, and British Museum (Natural History). Seventy-four species of ophiuroids are now known from southern Australia between Cape Howe, Victoria (37°30.1'S) and Cape Naturaliste, Western Australia (33°30.1'S) (Clark 1946, Baker 1981, and this paper).

In the course of studying Australasian Ophiuroidea in the past few years we have ex-

amined recent collections made by trawling expeditions (H.M.A.S. Diamantina and Kimbla, M.V. Aquarius, and M.V. Sarda) and divers working along the coasts of Western Australia, South Australia, Victoria, and Tasmania. Among these collections are a number of species previously unknown in the region, including two new species and others hitherto known only from other Pacific localities, particularly New Zealand. Some of these have been discussed by Baker (1979, 1980), and the remainder are reported here.

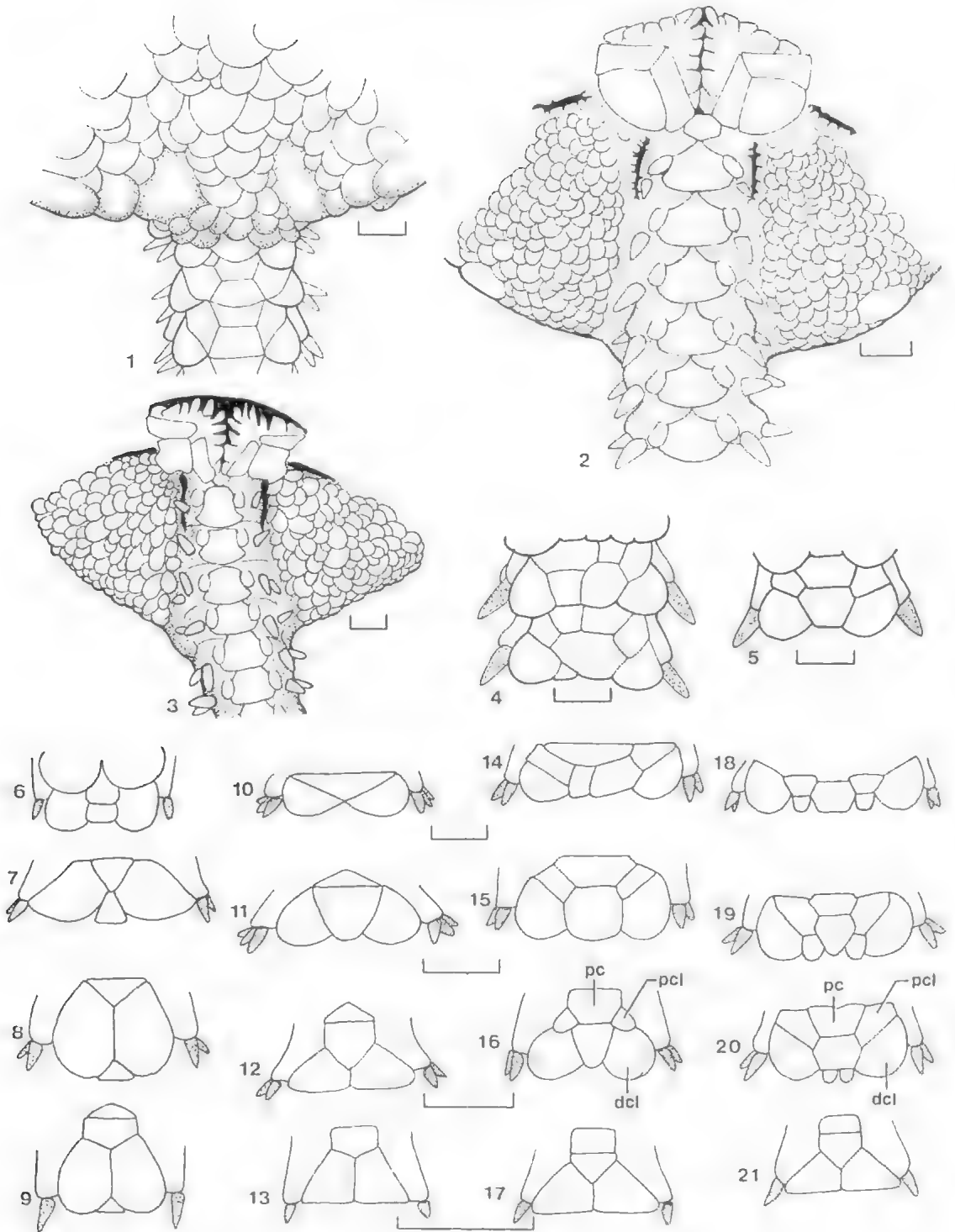
During visits to the South Australian Museum, one of us (A.N.B.) re-examined some of the ophiuroid material recorded by H. L. Clark (1928), and re-illustrated, by camera lucida drawings, several holotypes of local species described but not figured in detail by that worker. Our studies have shown that some taxonomic changes are necessary, and we have included such information in this paper.

Text conventions

The following abbreviations are used: *Institutions*: AM—Australian Museum, Sydney, BM(NH)—British Museum (Natural History), London. BPBM—Bernice P. Bishop Museum, Honolulu, Hawaii. MCZ—Museum of Comparative Zoology, Harvard. MNB—Museum für Naturkunde, Berlin. NMNZ—National Museum of New Zealand, Wellington. NMV—National Museum of Victoria, Melbourne.

* National Museum of New Zealand, Private Bag, Wellington, New Zealand.

† Bernice P. Bishop Museum, P.O. Box 19000-A, Honolulu, Hawaii.



SAM—South Australian Museum, Adelaide
WAM—Western Australian Museum, Perth
ZMH—Zoologisches Museum, Hamburg. ZMC
—Zoologisk Museum, Copenhagen. *Morpho-*
logy: d.d.—disc diameter.

Systematic Account

FAMILY Ophiuridae

Subfamily Ophiolopidinae

Ophioceres Koehler, 1922

Ophioceres hispinosus (H. L. Clark) n. comb.

FIGS 1–3, 5, 14–17

Ophioplocus hispinosus H. L. Clark, 1918: 337,
pl. 4, fig. 2; 1946: 275. A. M. Clark, 1966:
327. Dartnall, 1980: 43.

Specimens examined: Holotype, MCZ 4025,
Phillip Is. Westernport, Vic., no depth, May, 1915;
2, NMNZ 2074, Port Macdonnell, S.A., 3–4 m
29.iii.1964; 1, NMNZ 2076, West Id, S.A., 4 m,
29.i.1975; 2, NMV, H366, Cape Liptrap, Vic.,
no depth, 24.ii.1979; 2, NMNZ 2075, Fluted
Cape, Bruny Id, Tas., 13 m, 10.ii.1972; 1, NMNZ
2702, Deal Id, Tas., 20 m, 4.v.1974.

Remarks: These specimens range 3–9.5 mm
d.d., and have arms up to 3.3 × d.d. long.
They are thus similar to the type series in
dimensions.

That this species belongs in *Ophioceres*
rather than *Ophioplocus* is shown by the pre-
sence of one tentacle scale to each pore, short
genital slits originating close to the oral shield
and hardly extending past the first ventral arm
plate, and the relatively small amount of frag-
mentation of the dorsal arm plates (<10
pieces). In *Ophioplocus* Lyman, there are 3–6
tentacle scales, genital slits which are separated
from the oral shields by small platelets or scales
and which extend as far as the fourth segment,
and extensive dorsal arm plate fragmentation
(<20 pieces).

As pointed out by H. L. Clark (1918), this
species is extremely close to *O. huttoni* (Far-
quhar) from New Zealand. Examination of 15
specimens of the latter (NMNZ) shows small
but consistent differences which we consider

to be specific. Clark's suggestion that the num-
ber and arrangement of dorsal arm plate frag-
ments is different in these two species is cor-
rect, but only for the basal and middle part of
the arms. To confuse matters, however, the
basic pattern of fragmentation may be altered
by irregular secondary division of plates on
some or all arms of some specimens. The
dorsal arm plates consist of three main ele-
ments—a central plate bordered by two lateral
plates. The central plate is usually divided
transversely, and on the extremities of the
arms, the arrangement is virtually identical in
both species (Figs 17 & 21). Nearer the disc,
the lateral plates become separated from the
proximal portion of the central plate by an
oblique plate on each side (Figs 16 & 20). At
this stage of fragmentation, a difference be-
tween the two species is evident—in *huttoni*
the pair of additional oblique proximal centro-
lateral plates (pcl) nearly as wide as the distal
centro-laterals (del) and fully in contact with
the lateral edge of the proximal central plate
(pc), becomes wedged between the proximal
centro-laterals and the distal central plate; in
hispinosus however, the additional pcl plates
are usually less than $\frac{1}{2}$ the width of the del
plates and only in contact with the posterior
lateral portion of the pc plate. On the same arm
segment, and even more pronounced on proxi-
mal segments (Figs 15 & 19), the latter species
does not develop a third pair of plates distad
or disto-lateral to the dep as seen in *huttoni*
(Figs 16 & 20, 15 & 19). Occasionally, irregu-
lar longitudinal splits occur on the very basal
arm plates of *O. hispinosus* (Figs 4 & 14).

The oral shields also differ in proportions—
in *hispinosus* they are noticeably wider than
long ($w = 1.44$ – $1.63L$), whereas in *huttoni*
they are about as wide as long ($w = 1.05$ –
 $1.13L$).

Although there is no noticeable difference
in the arrangement of the disc scales, the radial
shields and marginal inter-radial plates are
larger in *hispinosus* than in *huttoni*. In fact the
size of the plates rival those in *O. marginata*
Fell, a second New Zealand species, regarded

Figs 1–21. 1, arm base and adjoining disc, dorsal, of *Ophioceres hispinosus* (NMNZ 2074); 2, same,
ventral; 3, arm base and adjoining disc, ventral, of *Ophioceres incipiens* (NMNZ 2715); 4, 6th
& 7th arm segments of *O. hispinosus* (NMV H366); 5, 6th arm segment of *O. hispinosus* (hola-
type MCZ 4025); 6–9, 2nd, 8th, 18th and distal arm segments of *O. incipiens* (NMNZ 2715);
10–13, same segments of *O. marginata* (NMNZ 2705); 14–17, same segments of *O. hispinosus*
(NMNZ 2074); 18–21, same segments of *O. huttoni* (NMNZ 1183). Abbreviations: pc—proximal
central plates; del—distal centro-lateral plates; pcl—proximal centro-lateral plates. Scale lines 0.5
mm.

here as valid (see Pawson 1969). This species can be distinguished from *bispinosus* and *huttoni* by its shorter arms ($2 \times$ d.d.), simpler pattern of arm plate fragmentation (Figs 10–13), shorter genital slits, and 3 instead of 2 arm spines on each segment. Unlike the other species, *O. marginata* is viviparous—a 9.0 mm d.d. specimen dissected during this study contained 18 juveniles 1–1.3 mm d.d.

The fourth species and type species, *O. incipiens* Koehler, also has a simple pattern of arm plate fragments (Figs 6–9), but has arrowhead-shaped oral shields (Fig. 3), 2 very short arm spines, and relatively long ($3.3 \times$ d.d.) arms.

The four *Ophioceres* species are restricted to the southern hemisphere antarctic, subantarctic, and cool temperate waters. *O. incipiens* is circumpolar in antarctic waters; *marginata* subantarctic New Zealand, and southern mainland New Zealand, *huttoni* northern New Zealand, and *bispinosus* southern Australia. *Ophioceres* species are recorded at depths of 0–384 m.

Ophiomusium Lyman, 1869

Ophiomusium anisacanthum H. L. Clark

FIGS 22–24

Ophiomusium anisacanthum H. L. Clark, 1928: 445, figs 133a, b; 1946: 247.—Baker, 1979: 31. *Specimens examined*: Holotype, SAM K254, and 2 paratypes, K256, Spencer Gulf or Gulf St Vincent, S.A.; 4, WAM 896–898–77, $31^{\circ}00'S$, $114^{\circ}51'E$, W of Lancelin, W.A., 130–160 m, HMAS Diamantina stations 41, 44.

Remarks: The Western Australian specimens of *O. anisacanthum* range 11–12 mm d.d., with arms 40 mm long, and are thus comparable with H. L. Clark's type series of five—the only other examples hitherto reported. Clark (1928) characterized this species by its single, large ventral inter-radial plate and one large arm spine in a series of three or four smaller spines. In the six specimens examined here, we find mostly four spines on the basal seven or eight segments. They grade in size from the lowermost, which is 0.5–0.75 as long as the segment bearing it, to the uppermost, which is 0.2 as long as a segment. The two lowermost spines are distinctly separated from the uppermost pair (Fig. 24). Beyond the seventh or eighth segment, only the lowermost pair are present. It is this arrangement of arm spines, plus the large inter-radial plate and the smooth, closely adpressed dorsal disc plates, that distinguish the species.

The type specimens are without exact locality or depth, Verco's label bearing no more than

"Spencer or St Vincent Gulfs". H. L. Clark (1946) expressed interest in the depths at which *anisacanthum* might eventually be found, for the genus is essentially a deep water one, and the South Australian gulfs are less than 55 m deep. It is thus of considerable interest that the species has now been collected off the Western Australian coast in 130–160 m, showing that *O. anisacanthum* is indeed one of the few species in this genus to inhabit the continental shelf.

Ophiomusium australe (H. L. Clark)

FIGS 25–27

Ophiomusium simplex var. *australe* H. L. Clark 1928: 449, fig. 135; 1946: 274–5.

Ophiomusium aporum H. L. Clark, 1928: 447, fig. 134; 1946: 275.

Ophiomusium australe.—Baker, 1979: 30.

Specimens examined: 9 from Vic., S.A. and W.A. (listed in Baker 1979, p. 30), 3, NMV H367 $38^{\circ}46'S$, $141^{\circ}33'E$, 155 m, 26.viii.1975.

Remarks: This southern Australian species has been discussed by Baker (1979). The opportunity is taken here to give a detailed illustration of the holotype (SAM K256).

FAMILY Ophionereididae

Ophionereis Lütken, 1859

Ophionereis terba n.sp.

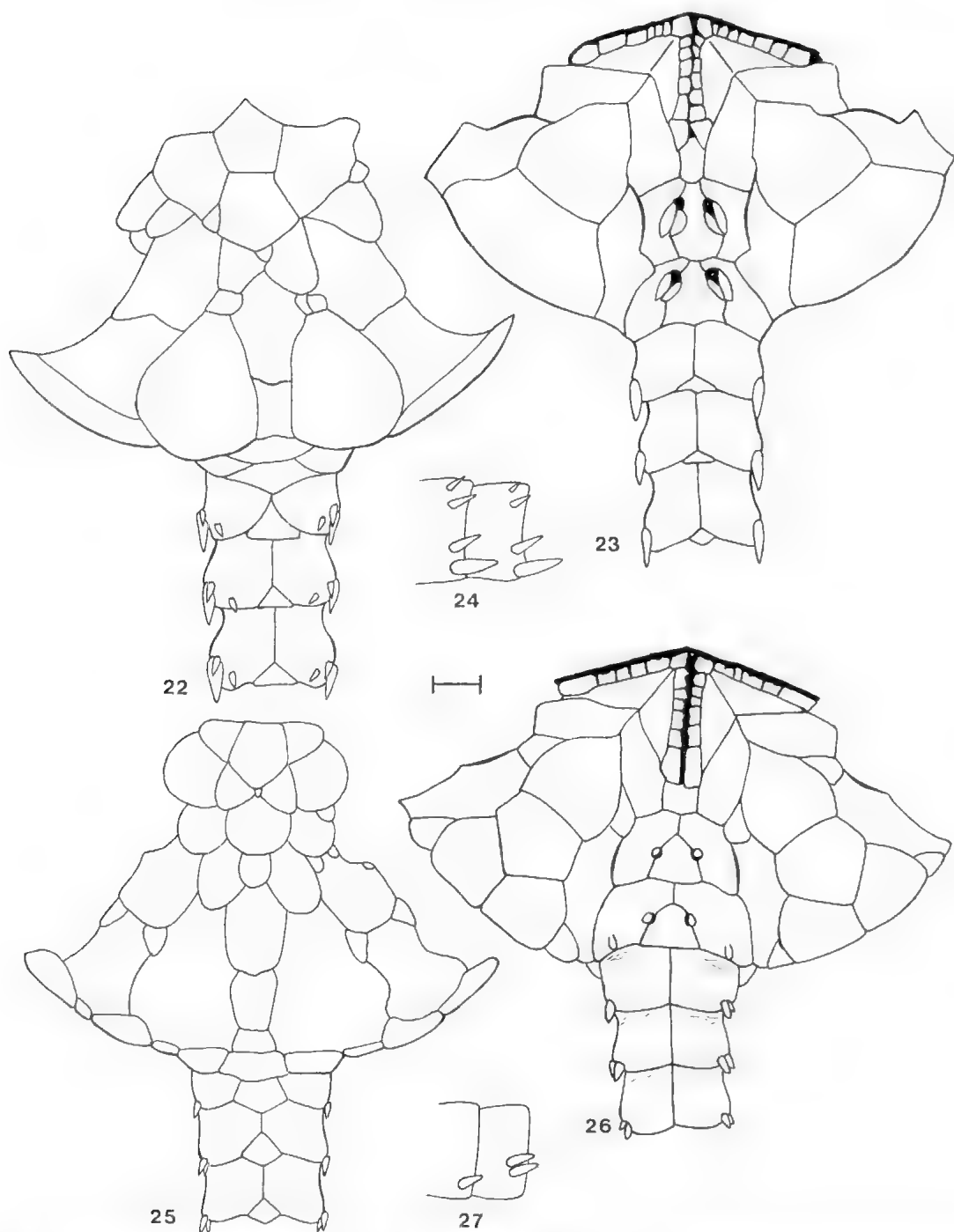
FIG. 30

Specimens examined: Holotype NMV H363 & paratype, NMNZ 3673, 43 km SSW Portland, Vic., 585 m, coll. R. Plant & M. Gomon, 14.v. 1979; paratypes 4, NMV, W of Cape Nelson, Vic., 164–201 m, June 1969; paratypes 2, NMNZ 1881, S of Warnambool, Vic., 220–310 m, 14.v. 1969.

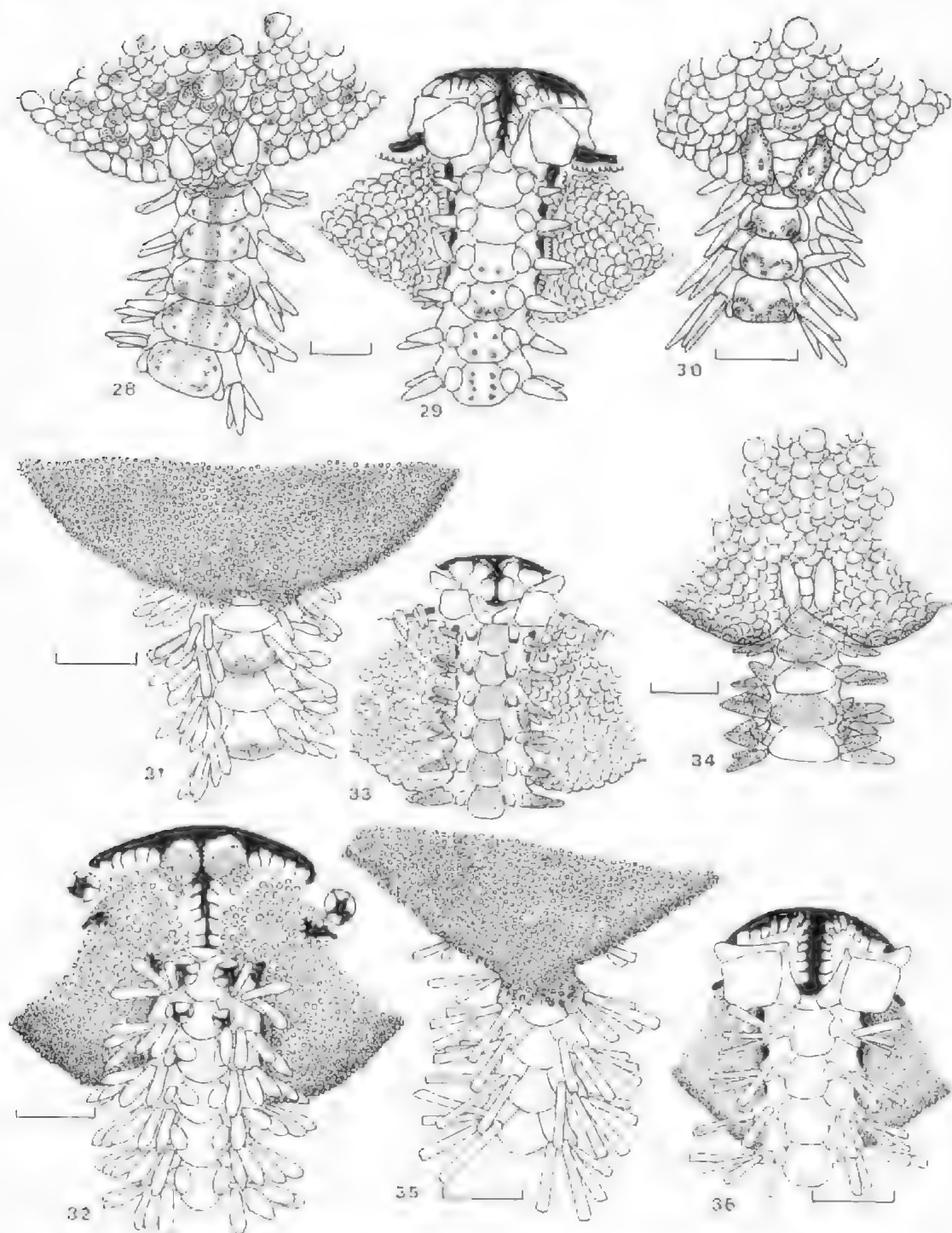
Description of holotype: Disc diameter 6.0 mm, arms broken but $c.9 \times$ d.d. Disc entirely covered with coarse imbricating scales, 3–4 in 1 mm radially; primaries prominent, and 1 central marginal inter-radial scale with 4 larger scales each side. Radial shields 0.9 mm long, 0.4 mm wide, divergent. Genital papillae small, granular, visible near arm bases dorsally.

Oral shields longer than wide, diamond-shaped with incurved disto-lateral margins. Adorals meeting within, attenuated distally. Distal oral papilla large, triangular, remaining 3 narrow, blunt.

Dorsal arm plates widest proximally, with evenly curved distal and proximal margins; supplementary plates very small and present throughout arm. Ventral arm plates widest distally, as long as wide, concave laterally, with



Figs 22-27. 22, arm base and adjoining disc, dorsal, of *Ophiomusium anisacanthum* (holotype SAM K254); 23, same, ventral, 24, 1st & 2nd lateral arm plates of SAM K254; 25, arm base and adjoining disc, dorsal, of *Ophiomusium australe* (holotype SAM K256); 26, same, ventral; 27, 1st & 2nd lateral arm plates of SAM K256. Scale line 0.5 mm.



Figs 28–36, arm bases and adjoining discs 28 & 29, *Ophioneereis lingata* (holotype, MCZ 5829) dorsal & ventral; 30, *Ophioneereis torchi* n. sp. (holotype, NMV H363), dorsal; 31 & 32, *Ophioconis apicatus* (NMNZ 2690) dorsal & ventral; 33 & 34, *Ophiactis tentaculata* (holotype SAM K213) ventral & dorsal; 35 & 36, *Ophiocomina australis* (BPHM W1822) dorsal & ventral. Scale lines 1.0 mm.

a straight distal margin curved only at the corners. Tentacle scales large, oval. Three slender, evenly tapered arm spines, middle spine longest, up to $2 \times$ length of adjacent ventral arm plate.

Colour pattern (dry): disc mottled brown and cream, brown pigment around edges of disc scales and radial shields. Dorsal arm plates with m-shaped brown band on distal margin (Fig. 30); ventral surface uniformly cream.

Remarks: This species is closely related to *O. lineata* H. L. Clark from north Queensland waters. It differs from it (Figs 28–29) in having relatively longer and more slender arm spines—in *lineata* they are only slightly longer than an adjacent ventral armplate, and are thick for their length. Also, the oral shields of *O. terba* are symmetrically diamond-shaped rather than blunt, spearhead-shaped as in *O. lineata*. The colour patterns of these two species provide the most readily observable distinguishing features: *O. terba* has very prominent m-shaped brown bands across the distal part of the dorsal arm plates, and has a uniformly cream ventral arm surface, whereas *O. lineata* has a single longitudinal dark line on the arms dorsally, and random dark spots on both arm surfaces (Figs 28–29 of the holotype, MCZ 5829).

No depth was given for the collection site of *O. lineata* by Clark (1946), but the waters surrounding Lindeman Island are 37–55 m. The bathymetric range of the new species is, in contrast, 164–585 m.

Apart from its striking colour pattern, the new species is characterized within *Ophionereis* by the coarse disc scaling the very small supplementary dorsal arm plates. The trivial name *terba* is an Australian aboriginal word meaning pretty, and alludes to the colour pattern.

Ophiichiton Lyman, 1879

Ophiichiton lentus Lyman

Ophiichiton lentus Lyman, 1879: 55, pl. XIV, figs 398–400. Baker, 1979: 34.

Specimens examined: 3, NMV H368, $38^{\circ}3.4'S$, $149^{\circ}23.7'E$, E of Flinders Id, Bass Strait, 183 m, 22.xi.1973; 1, NMV H360, $39^{\circ}32.5'S$, $148^{\circ}51.5'E$, 274 m, 24.xi.1973.

Remarks: The specimens are 5.0–6.5 mm d.d. and differ slightly from the 13 mm holotype: the primary disc scales are prominent, there are no papillae along the edges of the genital slits, and there are two tentacles scales only on the

first or second pore on each arm. These differences may be attributed to the juvenile nature of the specimens, for otherwise they agree closely with Lyman's description.

Ophiichiton lentus is the first representative of the genus to be found in Australian waters; the species is otherwise known from the type locality near the Kermadec Islands (also reported from there by Baker 1979) and the Chatham Rise, east of New Zealand in depths of 300–900 m.

FAMILY Ophiocomidae

Ophiocomina Koehler, 1922

Ophiocomina australis H. L. Clark

FIGS 35, 36, 63–68

Ophiocomina australis H. L. Clark, 1928: fig. 124; 1946: 188; A. M. Clark, 1966: 327.

Specimens examined: Holotype, SAM K211, outer Gulf St Vincent S.A., no depth; 4 BPBM W1822, 2 km W of Outer Harbour, Gulf St Vincent S.A., among *Posidonia* roots, 12 m depth, 3.iii. 1965.

Remarks: The additional specimens from Gulf St Vincent are the first to be recorded since H. L. Clark's original description. They range 5–8 mm d.d. This rare species has a very restricted distribution in the South Australian gulfs—extensive collecting along other parts of the southern coast by S. A. Shepherd and Mrs J. E. Watson have failed to locate other examples. The holotype is in poor condition, and because the species has not been adequately illustrated, we give here figures of an 8 mm d.d. BPBM specimen (Figs 35–36), and SEM photographs of the oral plates, dental plate, vertebra, and arm spine (Figs 63–68).

Wilkie (1980) proposed that *Ophiocomina*, with the species *australis* and *nigra*, be placed in the family Ophiacanthidae. It is our opinion, that there are better grounds for continuing to retain this genus in the Ophiocomidae. Among these grounds are the features of *Ophiopertis*, *Clarkcoma*, and other ophiocomids which are also found in *Ophiocomina* (Table 1). Furthermore, differences rather than similarities between *Ophiocomina* and *Ophiolimna* spp. in terms of the length: height ratio of the oral plates, shape of the lateral arm plates and, at least in one species of *Ophiolimna* examined (*O. cf. perfida*), the presence of an oral calcified ridge to enclose the radial water canal in the 2nd rather than the 1st arm vertebra, are considered features that do not indicate family resemblance between the two genera.

TABLE 1. Comparison of Ophiocomina with Ophiacanthids and Ophiocomids.

	<i>Ophio-</i> <i>comina</i>	<i>Ophio-</i> <i>pleris</i>	<i>Clarkcoma</i>	<i>Ophia-</i> <i>canthids</i>	Other ophio- comids
ORAL PLATES					
A. With radiating indentations on abradial muscle scar	—	—	—	—	+(-) ¹
B. Abradial muscle scar with flaring aboral wing	—	—	+		+
C. Adradial muscle scar less than (-), equal to (\pm), more than (+) half height of plate*	—	—	—	—, \pm	+, —
D. Longer than high (+), equal (\pm), higher than long (-)	\pm , +	+	—	+	—, \pm
E. Adradial articular area with upper distal edge rounded (+) or straight (-)	+	—	—	+, —	
TEETH					
Hyalinated tips	—	—	+	—	+
ARM SPINES					
Hollow (lumen more than half wall diameter)	+	—	+	+	-(+) ²
DENTAL PLATE					
A. Foramina	—	+	+	—	+
B. Oral end widest	+	+	+	+, —	+
C. Papillae present	+	+	+	-(+)	+
RADIAL SHIELD AND GENITAL PLATE ARTICULATION					
Two condyles and one pit	+	+	+	+, —	+

* length = proximo-distal axis
height = oral-aboral axis

¹(-) for *Ophiocoma pusilla*, *Ophiop-sila*, *Ophiocoma*, *Ophiomella*

²(+) for *O. pusilla* and *Ophiomastix ornata*.

³(+) for *ophiocoma longispina*, *O. pusilla* and *Ophiomastix variabilis*.

FAMILY Ophiidermatidae

Genus *Ophiocoma* Lütken, 1869

Ophiocoma opacum (H. L. Clark) n. comb.

FIGS 31, 32

Ophiurodon opacum H. L. Clark, 1928: 440. figs 132a & b, 1946: 255; A. M. Clark, 1966: 327.

Specimens examined: Holotype, SAM K243, "St Vincent or Spencer Gulfs", S.A. no depth; 1, NMNZ 2122, Upper Spencer Gulf, S.A., 11 m. 4.ix.1973; 1, NMNZ 2690, Upper Spencer Gulf, S.A., 18 m. 11.ix.1973; 1, NMNZ 2123, off Glenelg, S.A., artificial reef site, 3-4 m. 1972; 1, NMNZ 2722, W of Outer Harbour Gulf St Vincent, S.A., 5 m. 3.i.1965; 2, BPBM W2220 & WAM 31-74, Cockburn Sd, W.A. under stones, 0-2 m. 13.ii.1972; 2, WAM 1133-74, 3.2 km NW Busselton Jetty, W.A., *Posidonia*, *Cymodocea* & sand, 22-24 m. no date.

Remarks: H. L. Clark (1946) referred three Australian species to *Ophiurodon*. *O. opacum* was separated from its northern congeners (*cineta* and *permixta*) by having blunter, flat opaque upper (at least) arm spines. However,

A. M. Clark (1965) found no generic distinction after comparing the type species of *Ophiocoma* (*O. forbesi*) with *permixta* and *cineta*. She did not consider *O. opacum* at that time and, in a 1966 key retained without comment *opacum* in *Ophiurodon*.

Comparison of specimens of the three known Australian species indicate they are indeed congeneric and should all be retained in *Ophiocoma*. They share the following characters: longitudinally striated arm spines; more than two tentacle scales on proximal segments; broadened hyalinated usually serrated distal ends of teeth; adoral shields nearly or actually meeting in front of oral shield; disc granulae covering all or most of the oral shields as well as exposed part of oral plates.

The six specimens found since 1965 are the first recorded since the type description. They range 3.0-6.5 mm d.d., and their characters confirm the distinctness of this southern species of *Ophiocoma*. It may be separated from the two northern Australian species by its flat, almost spatulate arm spines. Contrary to the

type description, *O. opacum* does have finely striated lateral arm plates but apart from that feature, the holotype and new material agree with H. L. Clark's description. Because H. L. Clark's illustration lacks detail, we give here a camera lucida drawing of NMNZ 2690 (Figs 31, 32) the holotype being not in a suitable condition for illustration.

The records of *O. opacum* from Western Australia extend the known range of the species westward from the South Australian gulfs; this extension and its shallow water habitat (0–24 m) indicate that it is probably more widespread on the southern coasts of Australia.

Bathypectinura H. L. Clark, 1909

Bathypectinura heros (Lyman)

Pectinura heros Lyman, 1879: 48 pl 14, figs 389–91.

Bathypectinura heros: H. L. Clark, 1909 129–30; Baker, 1979: 34.

Specimens examined: 1, SAM TK 3132, 37°58'–37°47'S, 139°49'–139°45'E. SW of Cape Buffon, S.A., 548 m, May, 1981; 2, NMV, 43 km SSW of Portland, Vic., 585 m, 14.V.1979.

Remarks: This large species (TK 3132 is 62 mm d.d.) has previously been recorded from off Bateman's Bay, New South Wales, and south of Norfolk Island (Baker 1979) in the Australian region. It has a worldwide distribution in 240–2960 m.

FAMILY Ophiacanthidae

Ophiacantha Müller & Troschel, 1842

Ophiacantha shepherdii n.sp.

FIGS 37, 38, 69–74

Specimens examined: Holotype, SAM K1750 & paratype BPBM W1831, Seal Rock, Encounter Bay, West Id, S.A., 24 m, on algae, coll. S.A. Shepherd, 18.ix.1967. Paratypes, 1, SAM E1749 & 1 NMNZ 3083, Deva Inlet, West Id, S.A., 18 m, coll. S.A. Shepherd, 24.vi.1967. Paratype, NMNZ, 11 km off Glenelg, Gulf St Vincent, S.A., 25 m, coll. S.A. Shepherd, 27.xii.1966. Paratypes, 8, NMNZ 3085, 2, BPBM W1835, Lund's End, West Id, S.A., 17–18 m, coll. S.A. Shepherd, 1967. Paratypes, 2, BPBM 1839, Seal Rock, West Id, S.A., 24 m, coll. S.A. Shepherd, 5.ii.1967. Paratypes, 2, WAM, 19–81, Oedipus Pt, West Id, S.A., 15 m, coll. S.A. Shepherd, no date; Paratypes, 1, AM, 1, BM(NH), 4, NMNZ 3641, Middle Pt, Cape Northumberland, S.A., 13 m, in algae, coll. S.A. Shepherd, 19.iii.1974.

Description of holotype: Disc diameter 2.5 mm; arm length 11–12 mm, arms taper gradually. Upper side of disc with very low conical granules (rarely as high as broad),

slightly larger and more prominent inter-radially than radially; granules generally not contiguous, underlying scales evident between them. Radial shields sock-shaped, distal ends exposed and adjacent to lateral edge of first exposed dorsal arm plate; also in contact with genital plate below. On lower side of disc, granules more widely spaced proximally; disc scales evident.

Oral shields approximately 1.5 × broader than long, somewhat triangular, with small lobe in distal edge, madreporitic plate much larger, with greater distal prominence. Adoral shields large, meeting broadly within, encroaching distad around most of ventral shield.

Three oral papillae on edge of oral plate; outer two longer than broad, similar in size to inner papilla which is more sharply tapered and apically directed. The first tooth level with oral papillae but larger and arrow-head shaped, other teeth not visible.

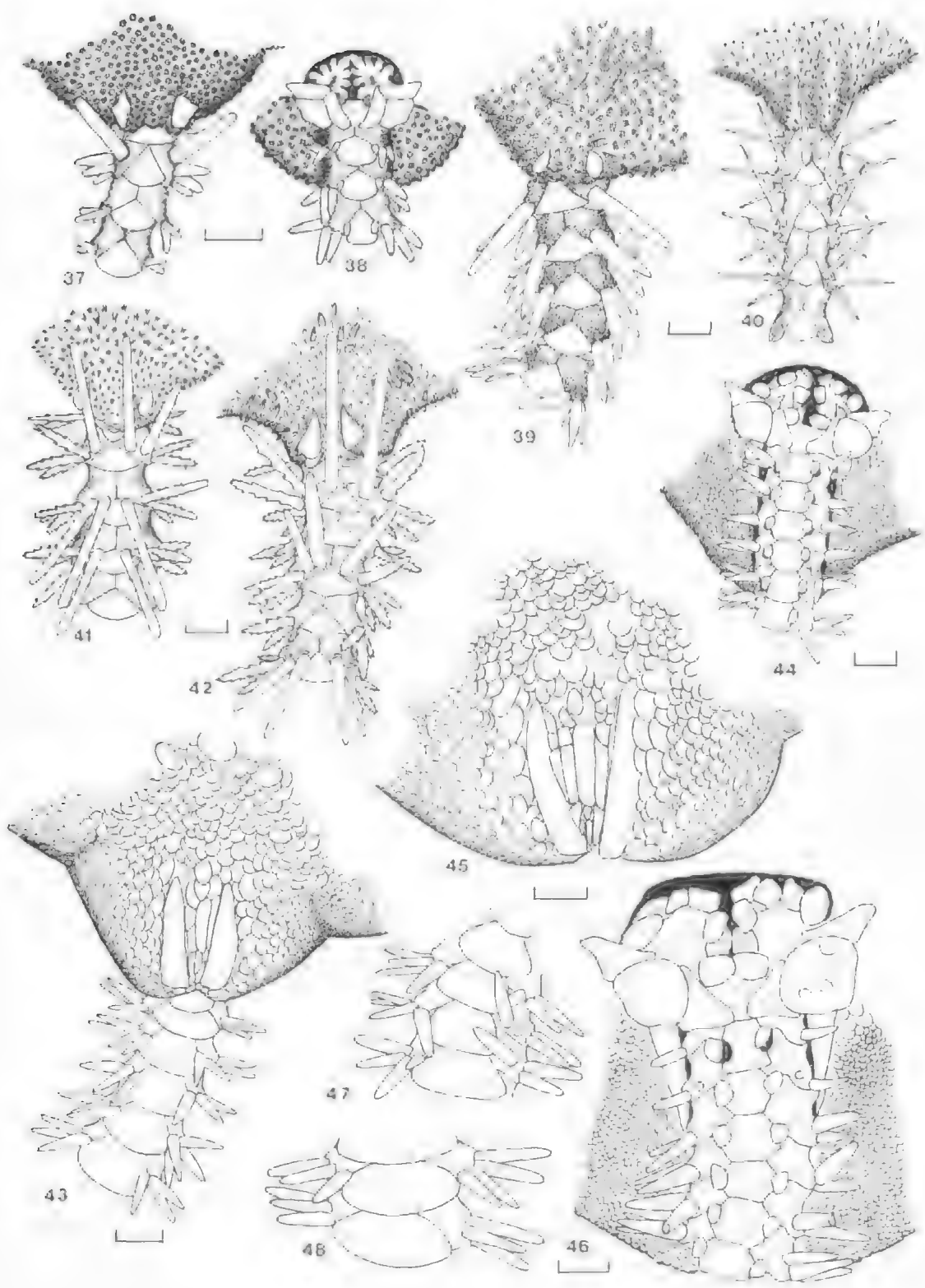
First ventral arm plates slightly broader than following plates which are fan-shaped, with the distal edge convex (Fig. 69); plates separated from one another by lateral arm plates, the separation increasing distally.

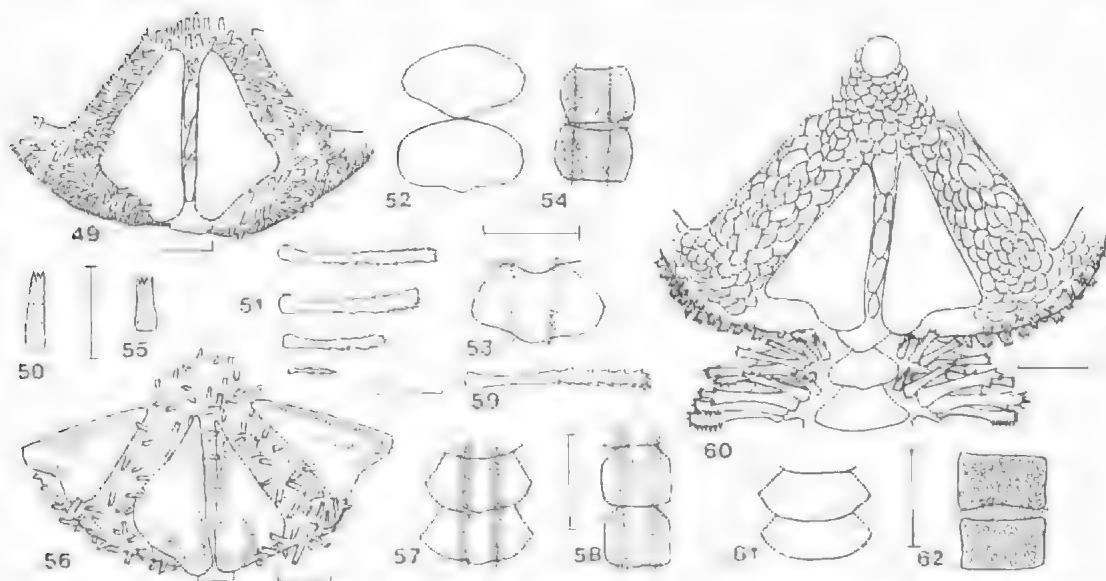
One tentacle scale, less than 1 a segment long, rectangular with rounded tip (Fig. 70); scales remaining approximately same size and shape on distal segments in contrast to diminishing size of other arm plates.

Dorsal arm plates broadly fan shaped, 1.5 × or more broader than long; with exception of the first exposed plate which is in contact with second plate, all others separated from each other by lateral plates. Micro-structure of these plates is a close mesh of pores and trabeculae, with smooth raised lumps at intersections of meshes (Figs 71, 72).

Lateral arm plates meeting broadly above and below; distal edge flaired considerably where arm spines attached. Two short and 3 somewhat longer bluntly rounded spines on segments one and two respectively; segment three (first free segment) with 4 arm spines, the lower three being somewhat longer than those of segment two, minutely spiculate and gently tapering, while upper spine on each side is greatly enlarged, 2 × length of adjacent lower spine (750 mμ vs. 350 mμ) and nearly twice as thick, microscopically rugose, scarcely tapering, and broadly rounded at tip (Fig. 73). One of 10 sides with only 3 arm spines, the upper enlarged spine being absent.

Three spines (rarely 4) continue on distal segments, the spines remaining short, blunt, in-





Figs 49-62. 49-54, *Ophiothrix* (*Placophiothrix*) *albostriata* (holotype, SAM K215): 49, radial disc segment, dorsal; 50, disc stump; 51, representative arm spines; 52, 5th & 6th dorsal arm plates; 53, 20th dorsal arm plate with pigment; 54, 9th & 10th ventral arm plates. 55-59, *Ophiothrix* (*Placophiothrix*) *lucocaudalea* (holotype, SAM K218): 55, disc stump; 56, radial disc segment, dorsal; 57, 5th & 6th dorsal arm plates with pigment; 58, 9th & 10th ventral arm plates with pigment; 59, uppermost basal arm spine. 60-62, *Ophiothrix* (*Kevstonea*) *hymenacantha* (holotype, SAM K217): 60, arm base and adjoining disc, dorsal; 61, 5th & 6th dorsal arm plates; 62, 9th & 10th ventral arm plates. Scale lines 1.0 mm.

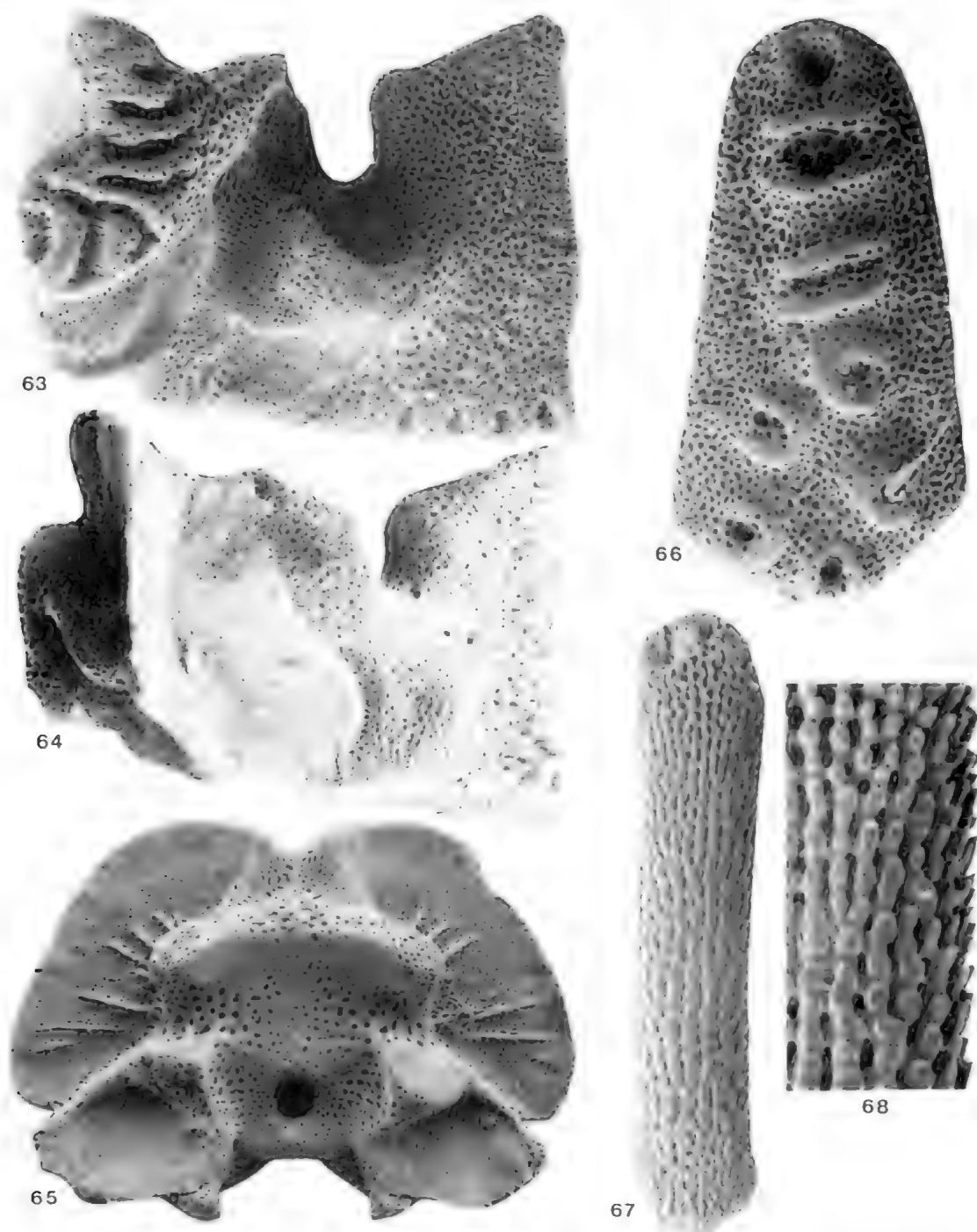
creasingly spiculate, and near end becoming dentate along one margin (Fig. 74).

Variation. A paratype (BPBM W1831) from the same station as the holotype is the largest specimen (d.d. of 2.7 mm). The arms are contorted and twisted upward making the upper side difficult to see. However, the lower (oral) surface, especially the mouth region, is fully exposed. In contrast to the holotype, this specimen has the adoral shields separated in front of the oral shields, probably due to the flexure of the upwardly directed arms. The teeth are visible, there being 2 or 3 below the apical one, somewhat blunt to slightly tapered or, in two cases, the upper being elongate and pointed. At the inner radial edge of each side of the ventral arm shield there is a small papilla which is separate from either the adoral shield or jaw plate. None of the other specimens has this

feature. An arm spine sequence of 2-3-4-3-3 is typical on the first five proximal segments. Four arm spines occur very infrequently (seg. 6, on one side of one arm and seg. 7, on both sides of one arm, one side on another) but in no case are these enlarged like those on segment 3. The smallest specimen (d.d. 1.5 mm) shows only a few sides of segment 3 with the fourth spine developed and only on two sides are these enlarged. The largest specimen has a few enlarged granules about as high as broad located in the inter-radial oral region. It is quite evident that a distal lobe of each adoral shield separates the oral shield from the first lateral arm plates in this specimen. In the holotype this lobe is not as well developed and the oral shields touch the first laterals.

Remarks: *Ophiacantha shepherdii* differs from congeners in having the combination of low

Figs 37-48. 37, arm base and adjoining disc, dorsal, of *Ophiacantha shepherdii* n. sp. (holotype, SAM K1750); 38, same, ventral; 39-42, arm bases and adjoining discs, dorsal, of: 39, *Ophiacantha heterocela* (NMNZ 2071); 40, *Ophiacantha brachygnatha* (NMNZ 2070); 41, *Ophiacantha clavagera* (NMNZ 2072); 42, *Ophiacantha alternata* (NMNZ 2087); 43, arm base and adjoining disc, dorsal, of *Amphiprora trisacantha* (NMNZ 2073); 44, same, ventral; 45, radial disc segment, dorsal, of *Amphiprora trisacantha* (holotype, SAM K212); 46, same, ventral; 47 & 48, basal, & 9th & 10th arm segments of *A. trisacantha*, holotype. Scale line 0.5 mm.



Figs 63–68. *Ophiocomina australis* (BPBM W1822): 63, oral plate, adradial view, x81; 64, oral plate, abradial view, x72; 65, 1st arm vertebra, x187; 66, dental plate, x117; 67, arm spine, x89; 68, edge of arm spine, x250.

blunt disc granules and only one pair of smooth, elongate and enlarged upper arm spines on the segment next to the disc. The granules on *O. shepherdii* are rarely as high as broad (spinules are defined as disc elements $2 \times$ as high as broad, with granules up to $2 \times$ or less as high as broad, with blunt tips). Whereas *O. gracilis* (Studer) shows a similar pronounced elongation of one pair of basal upper arm spines, these and other arm spines differ from those of *O. shepherdii* by being acutely tapered to sharp points, and the disc covered by delicate multifid pointed disc elements. *O. alternata* A. M. Clark, which has been collected with *O. shepherdii*, differs by having short conical granules mixed with longer, thicker blunt spinules on the disc, an alternating sequence of arm spines, and segment 1 with three, or sometimes four, arm spines (vs. two, rarely three, on this segment in *O. shepherdii*). *O. heterotyla* H. L. Clark, in contrast to *O. shepherdii*, carries five rather than four spines on the basal free segment and the upper arm spine of the first free basal segment is much less than twice that of the preceding spine in the row, and all the spines taper evenly towards the tip.

O. shepherdii is further characterized by having microscopically smooth dorsal arm plate trabeculae on fan-shaped plates, oral shields which are separated from the first lateral arm plates by a distal lobe of the adoral shields (at least in the largest specimens), and short (except for one pair of upper), few (not more than four) smooth arm spines, the rows not approximate dorsally.

This species is named for its collector, Mr S. A. Shepherd.

Ophiacantha heterotyla H. L. Clark

FIGS 39, 75–78

Ophiacantha heterotyla H. L. Clark, 1909: 542, pl. 52, figs 4–6; 1918: 86; 1938: 209; 1946: 184.

Specimen examined: 1, NMNZ 2071, off Simpson's Bay, Bruny Id, Tas., 11 m, 18.ix.1972.

Remarks: About average size for this species (3.5 d.d., 13.0 mm arm length). Stout, rather club-shaped disc spinelets characteristic of *O. heterotyla* reach 0.5 mm long and are prominent radially between the radial shields and the disc centre. Elsewhere, the disc is covered by small, round, glassy plates bearing short, blunt stumps. There are 5 or 6 arm spines on the first two or three free arm segments, then 4 spines over the remainder of the arm. The

spines are stout, cylindrical, and the uppermost are initially the longest (Fig. 39), those on the first two segments being up to $2\frac{1}{2}$ arm segments long. After the 8th or 10th arm segment the lowermost spine is noticeably shorter than the other three. The micro-structure of the arm spines consists of a longitudinal series of granule-bearing, divaricating ridges separated by grooves and hollows (Fig. 75). The dorsal and ventral arm plates are roughly triangular and have a micro-structure similar to, but more random than, that of the arm spines (Figs 76–78). The tiny granules are not present on the ventral plates (Fig. 77).

Ophiacantha heterotyla is closely related to *O. alternata* and *O. shepherdii*. From the former it is distinguished by having a non-alternating number of arm spines on successive arm segments, and taller disc elements. From *O. shepherdii*, it differs in the greater number and size of basal arm spines, and the tall spinelets rather than low granules on the disc. The microstructure of the arm plates is closer to *O. alternata* than to the other South Australian congeners (Figs 78, 89).

O. heterotyla apparently has a restricted distribution from Sydney to Bruny Id, Tasmania in 9–146 m.

Ophiacantha alternata A. M. Clark

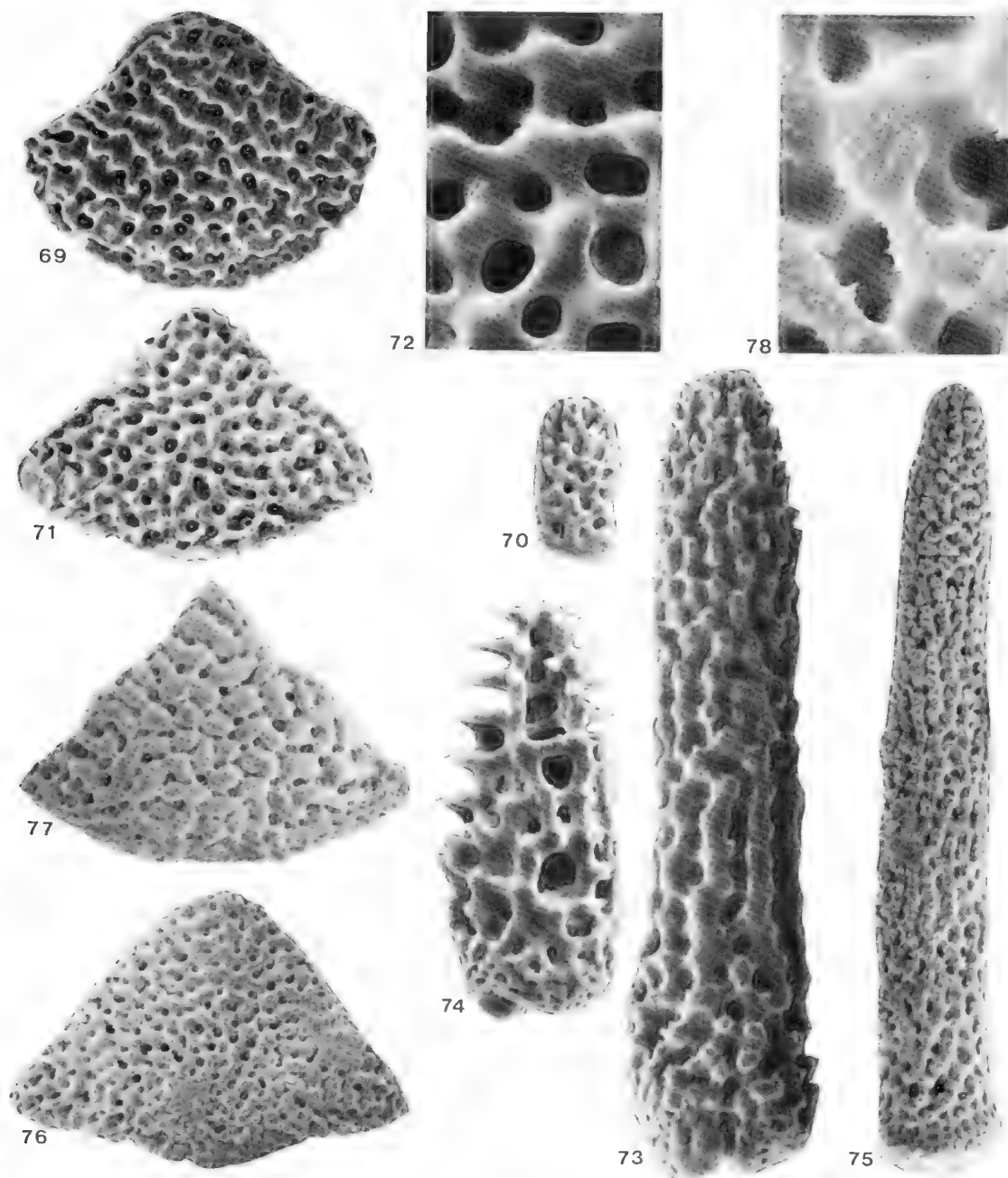
FIGS 42, 84–82

Ophiacantha alternata A. M. Clark, 1966: 328–330, Figs 4a–c.

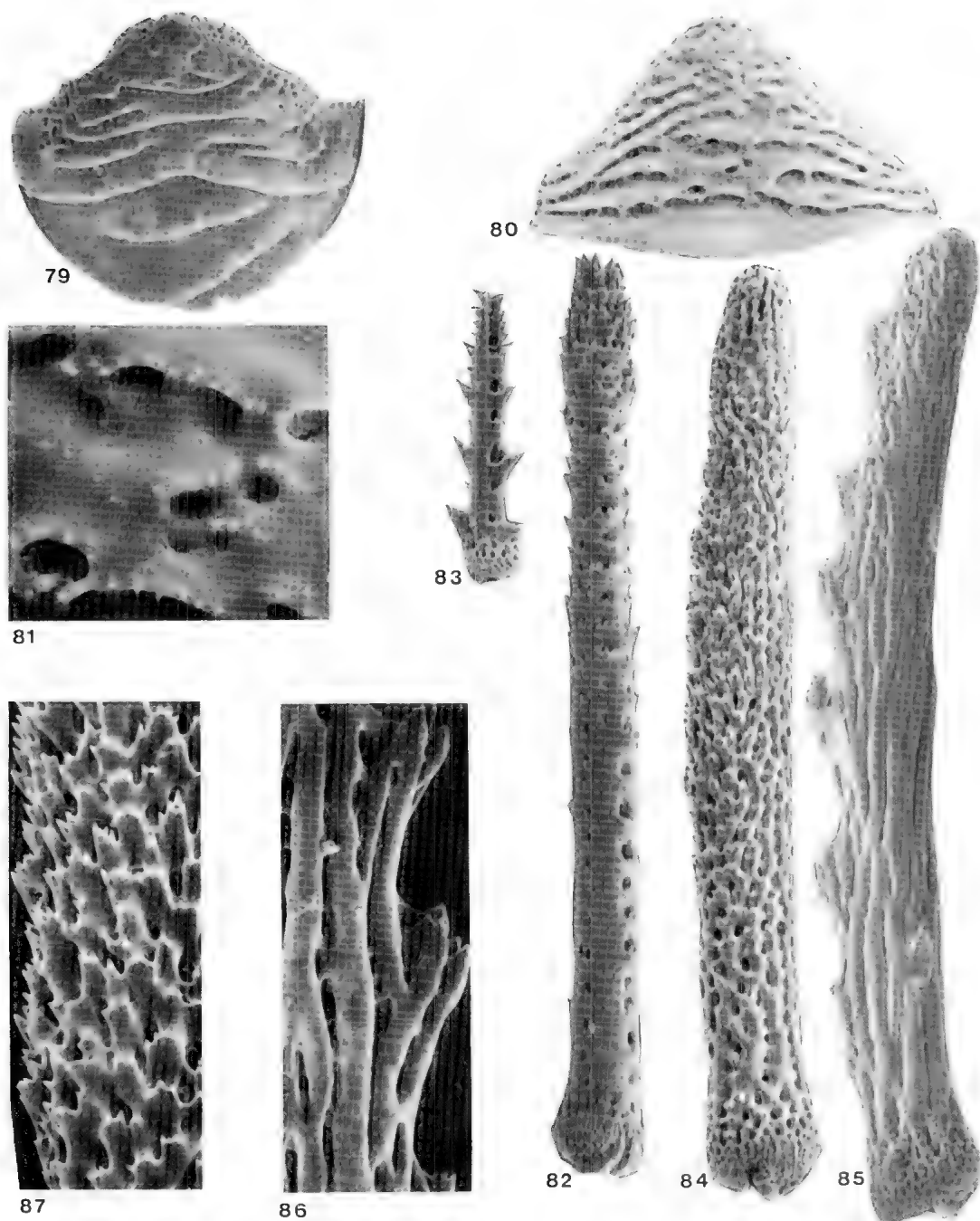
Ophiacantha clavigera Koehler: H. L. Clark, 1938: 208 (Koombana Bay, Bunbury, Western Australia—part).

Specimens examined: Paratypes, 3, NMV H16, Port Phillip Bay, Vic., 5.5–12 m 21.v.1961; 1, WAM 634–78, Arrawarra, N of Coffs Hbr, N.S.W., tide pool, 20.iii.1978; 1, NMNZ 2114, Port Hacking, N.S.W., 7 m, 30.v.1976; 6, NMNZ 2379, Erith Id, Kent Group, Bass Strait, 50 m, 6.v.1974; 1, NMNZ 2116, Westernport, Vic., 3 m, 2.v.1976; 2, NMNZ 2099, off Pt Marsden, S.A., 20 m, Jan., 1965; 12, NMNZ 2093–96, West Id, S.A. 2–27 m, 19.iii.1966–18.ix.1967; 1, BPBM W1810, 8 km N of Western River, Investigator Strait, S.A., 45 m, 12.i.1965; 4, NMNZ 2098, 11 km off Glenelg, S.A., 25 m, 27.xii.1966; 2, NMNZ 2100, Eagle Bay, Cape Naturaliste, W.A., 1–5 m, 24.ii.1975; 2, WAM 259–71, BPBM W2208, Cockburn Sound, W.A., no depth, 28.v.1958; 2, MCZ 4900, Koombana Bay, Bunbury W.A., no depth, 26.x.1929 (det. *O. clavigera* by H. L. Clark, 1938).

Remarks: Hitherto this species was known only from Port Phillip Bay, Victoria; the new



Figs 69–78. 69–74, *Ophiacantha shepherdii* (paratype NMNZ 3085): 69, 2nd ventral arm plate, x128; 70, tentacle scale x145; 71, 2nd dorsal arm plate, x108; 72, surface detail of 71, x435; 73, uppermost basal arm spine, x145; 74, distal arm spine, x217. 75–78, *Ophiacantha heterotyla* (NMNZ 2071): 75, uppermost basal arm spine, x72; 76, 2nd dorsal arm plate x72; 77, 2nd ventral arm plate, x77; 78, surface detail of 76, x580.



Figs 79–87. 79–83, *Ophiacantha clavigera* (NMNZ 2015): 79, 2nd ventral arm plate, x138; 80, 2nd dorsal arm plate, x136; 81, surface detail of 80, x 544; 82, uppermost basal arm spine, x90; 83, middle basal arm spine, x86. 84–87, *Ophiacantha alternata* (NMNZ 2097 & 2099): 84, uppermost basal arm spine of 2097, x80; 85, uppermost basal arm spine of 2099, x74; 86, surface detail of 85, x150; 87, surface detail of 84, x150.

material shows a wide southern Australian distribution from Coffs Harbour, N.S.W. (30° 18'S) to Cockburn Sound, W.A. (31° 57'S) in 1–45 m. This distribution pattern is shared by a number of endemic shallow water ophiuroids (*Conocladus australis*, *Clarkcoma canaliculata*, *Ophiopetu assimilis*, *Ophurachuella ramsayi*, *Ophiothrix* (*Placophiothrix*) *spongicola*), and supports the concept of a single southern faunal region in Australian coastal waters.

Ophiacantha alternata varies remarkably in the shape of its arm spines. The macroscopic appearance of the spines ranges from smooth to broadly serrate on one side (Figs 84, 85). The uppermost basal spines are usually more or less straight when smooth, although the tips may be slightly clavate or even bifurcate in rare cases. The laterally serrate spines are, however, invariably curved in a sabre-like fashion (Fig. 85). Microscopically, the spines are sculptured in two ways—the basal portions being an anastomosing system of smooth longitudinal ridges and pores (Fig. 86), whereas the distal portions are finely rugose, the ridges having become finely but irregularly covered with raised lumps bearing small thorns (Fig. 87). When present, the broadly serrate spines occur on all arms; and the adjacent smaller spines are similarly serrate, but bear teeth on both edges rather than one (Fig. 91). Were it not for the absence of another constantly different character, and the fact that individuals with smooth spines occur in samples with those bearing serrate spines, these two forms could be mistaken for separate species. In other respects specimens are alike. The microstructure of the dorsal arm plates is similar to *O. heterotyla*, with fine rugosities scattered over enlarged sections of the traheculae (Figs 88, 90), but that species can be distinguished from *O. alternata* because of the latter's alternating sequence of arm spines, a typical sequence being 3-3-7-8-5-7-5-6-4-6 on the proximal segments (NMV H16).

The radial shields of *O. alternata* are, like those of *heterotyla* and *shepherdi*, exposed only at their distal tips. The shape of these shields is unusual—they are "sock-like" (Fig. 92) rather than the long narrow and "bar-like" shields apparently typical of *Ophiacantha*.

Ophiacantha clavigera Koehler

FIGS 41, 79–83

Ophiacantha clavigera Koehler, 1907: 247, figs 1–3. — H. L. Clark 1938: 208 (in part); 1946: 184 (in part). — A. M. Clark, 1966: 330.

Specimens examined: 3, NMNZ 2105, 2089, 2373, Seal Rock, West Id, S.A., 16–27 m, Mar. & Aug., 1966, Feb., 1967; 1, NMNZ 2374, 11 km off Glenelg, S.A., 25 m, 27.xii.1966; 1, NMNZ 2085, off Waldengrove Id, Great Australian Bight, 23 m, 11.v.1971; 1, ZMH E2016 (herein designated lectotype), Stn 51, Cockburn Sd, S Channel, rocky bottom, 6.5–8 m, 30.ix.1905; 3, ZMH E6594, 2, MNH 4560, 1, WAM 4416 (herein designated paralectotypes), Stn 56, Koombana Bay, 9.6 or 11.2 km SW of Bunbury, W.A., rocky bottom with sparse plant growth, 14.5–18 m depth, 28.vi.1905; 1, ZMH E6123, Stn 50, Cockburn Sd, Southern Flats, seaweed, 3–4 m, 30.ix.1905; 5, MCZ 4900, Koombana Bay, W.A., no depth, 26.x.1929; 1, WAM 17–81, 11 km SW Bunbury, W.A., 20 m depth, 13.iv.1963; 5, NMNZ 3106, off Carnac Id, W.A., 7.5 m, 21.iii.1972; 1, WAM 517–77, 27 km W of Cape Peron, W.A., 35 m, 29.vi.1977; 1, WAM 18–81, ca. 18 km N of Dongara, W.A., 18.3 m, 16.ii.1976; 1, MCZ 4901, Broome, W.A., dredged, no depth, June 1929.

Remarks: The specimens range 1.5–3.5 mm d.d., with arms 4–5 × d.d. long, and agree well with Koehler's description and rather diagrammatic figures. The South Australian records are an extension of the species' range eastward from Western Australia where it has been reported from Cockburn Sound, Koombana Bay, and Broome (Koehler 1907, H. L. Clark 1938).

New morphological information on this species is now available from SEM examination of arm plates and spines (Figs 79–83). The surface of the ventral arm plates consists of a series of broad, smooth, transverse "shelves", beneath the edges of which are minute pores (Fig. 79). The dorsal arm plates have similar shelves, but they are somewhat crowded and irregular, and their edges bear minute thorns (Figs 80, 81). The longest upper arm spines are cylindrical and smooth basally, with two longitudinal rows of pores running towards a slightly swollen and thorny tip (Fig. 82). The lower arm spines are flattish, with a single row of pores, and strong teeth on their edges (Fig. 83). These features, plus a non-alternating sequence of arm spines, and forked, thorny disc elements, characterize *O. clavigera*.

Eight of the 11 specimens reported as *Ophiacantha clavigera* by H. L. Clark (1938) from Koombana Bay, Bunbury, and one from Broome were lent by MCZ. Three of the Koombana Bay specimens with d.d. 1.7 to 3.5 mm can be assigned to *O. alternata* A. M. Clark. They are easily distinguished from the other five by having a well defined alternating sequence of arm spines and conical, tuberculate

disc elements. Examination of the type specimens of *O. clavigera* in ZMH and MNB reveals the very characteristic thorny forked disc elements as originally shown by Koehler, noticeably white curved radial shields, and non-alternating sequence of arm spines. These characters are evident on the five other MCZ specimens reported by H. L. Clark as *O. clavigera* from Koombana Bay.

H. L. Clark's confusion between *O. clavigera* and *O. alternata* led to an error in his 1946 key to Australian *Ophiacantha* species. He considered *O. clavigera* among those species having the disc covered by coarse granules and short blunt spinules, and only the first free segment with long upper arm spines. *O. clavigera*, as Koehler figured clearly, has delicate, slender, forked disc spinules and elongate, often claviform (towards the tip), upper arm spines on at least four segments beyond the disc (Figs 41, 82).

In addition to failing to note the presence of a regularly alternating arm spine sequence for several of the specimens from Koombana Bay, H. L. Clark (1938) considered that *O. clavigera* exhibited "growth changes" with respect to the nature of the disc elements, remarking that "the disc spinelets tipped with 2 or 3 glassy teeth gradually lose those tips and become changed into little sugar-loaf shaped tubercles." In fact, however, one of these specimens with a d.d. of 1.7 mm, having conical tubercles and an alternating arm spine sequence, is smaller than several with forked thorny disc elements and non-alternating arm spines, and is unquestionably *O. alternata*. On no individual of *O. clavigera* examined does a mixture of the two kinds of disc elements occur.

Ripe orange gonads were observed protruding from a rupture below several radial shields in a 2.0 mm specimen (MCX 4900).

This species occurs mostly on algae in rocky areas, from the shallow sub-littoral to a known maximum depth of 35 m.

Lectotype designation. Koehler (1907, p. 247) reported "deux petits echantillons" from Cockburn Sound (Stn 51) and "cinq petits echantillons" from Koombana Bay (Stn 56). ZMH has 3 specimens labelled "Paratypes", MNB has 2 labelled "Types", and WAM has one labelled "Holotype", all from Stn 56. ZMH also has 1 specimen labelled "Holotype" from Stn 51 and 1 from Stn 50 labelled as "Cotype". Although Koehler did not select a holotype in

his original description of *Ophiacantha clavigera*, he mentioned the largest example from Cockburn Sound was 2.5 mm d.d. and, judging from the scale given, his Fig. 1 is of a specimen approximately that size. We have selected the ZMH specimen (E2016) from Stn 51 as lectotype because with a d.d. of 2.7 mm, it conforms closely with the size and original description, and remains in good condition in alcohol. The other specimens mentioned above are all smaller than 2.5 mm, and that from WAM is badly decalcified.

Paralectotype designation is established for the ZMH, MNB and WAM specimens from Stn 56 although it is not possible to resolve the discrepancy in number of individuals from Stn 56 (5 reported, 6 in collections). One of these might be one of the two presently not located from Stn 51. Cockburn Sound is now the type locality. The specimen from Stn 50 at ZMH with d.d. 2.0 mm has no type status.

Ophiacantha brachygnatha H. L. Clark

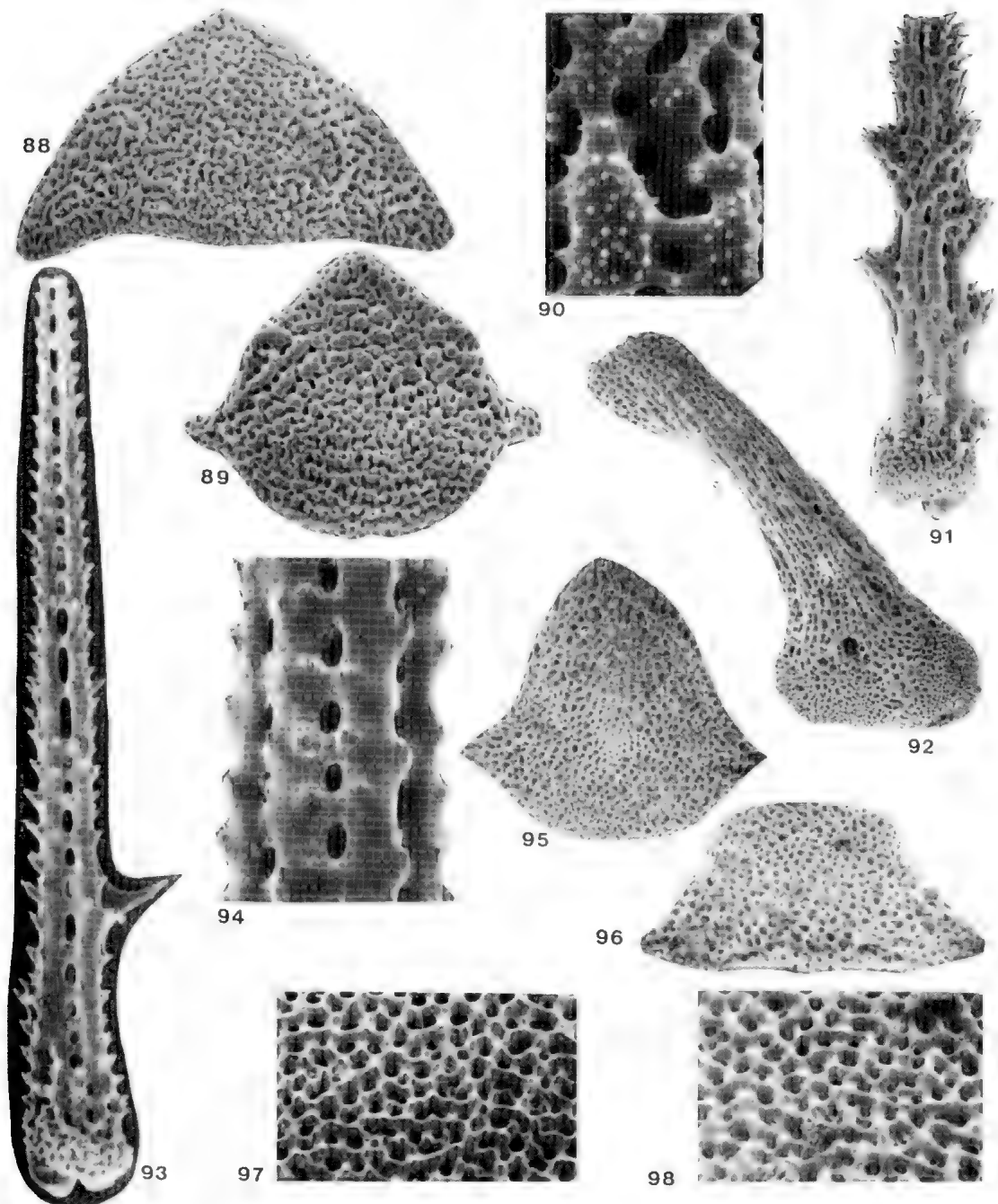
FIGS 40, 93–98

Ophiacantha brachygnatha H. L. Clark, 1928: 420, figs 123a & b; 1946: 186.

Ophiacantha abyssicola G. O. Sars var. *otagoensis* Fell, 1958: 25 pl. 4, figs, G, L.

Specimens examined: Holotype SAM K208, St Vincent or Spencer Gulfs, S.A., no date or depth; paratype, MCZ 4611, same locality data as holotype; 6, NMNZ 2084, S of Warrnambool, Vic., 220–310 m, 14.v.1969; 3, NMV H359, 39°44.5'S, 148°49'E, Bass Strait, 640 m, 24.xi.1973; 1, NMNZ 3570, West Id, S.A., 2 m, no date. 1, WAM 844–78, 31°45'S, 115°02'E, NW Rottnest Id, W.A., 265–276 m, 18.iii.1972; 8, WAM 235–78, + 3, BPBM W2597, 33°30'S, 114°31'E, W of Cape Naturaliste, W.A., 250–237 m 15.iii.1972; 1, WAM 222–78, 27°18'S, 114°06'E, NW of Bluff Pt, W.A., 99 m, no date; 10, NMNZ 2784, 45°46'S, 171°05'E, off Otago, N.Z., 660–600 m, 1974.

Remarks: Hitherto this species was known from the two type specimens from Spencer or St Vincent Gulfs. The new material, providing extensions eastward to Victoria, and New Zealand, and westward to Western Australia, is smaller (1.8–4.5 mm d.d., arms <6 × d.d.) than the holotype but agrees with it in all other details. *O. brachygnatha* is characterized by a disc cover of thin-stalked, flared multifid spinelets, moniliform arms bearing bell-shaped dorsal arm plates, and 5–7 narrow, tapering, finely serrated arm spines. The microstructure of the arm spines consists of parallel, longitudinal toothed ridges separated by single series



Figs 88–98. 88–92, *Ophiacantha alternata* (NMNZ 2099): 88, 2nd dorsal arm plate, x90; 89, 2nd ventral arm plate, x90; 90, surface detail of 88, x360; 91, middle basal arm spine, x72; 92, radial shield, x40. 93–98, *Ophiacantha brachygnatha* (NMNZ 2084 & 2034): 93, uppermost basal arm spine of 2084, x96; 94, surface detail of arm spine from 2034, x150; 95, 3rd dorsal arm plate of 2034, x100; 96, 2nd ventral arm plate of 2034, x80; 97, surface detail of 95, x100; 98, surface detail of 96, x100.

of evenly spaced perforations (Fig. 94). There is sometimes one large tooth on the abradial side of the largest spines, situated at about .3 of the spine length (Fig. 93). The external surfaces of the dorsal and ventral arm plates (Figs 95–96) are covered with perforations and trabeculae bearing sharp points and smooth lumps, respectively (Figs 97–98).

Ophiacantha abyssicola var. *otagoensis* from New Zealand, is a synonym of this species, but *O. abyssicola* s. str. appears to differ mainly in the characteristic cross-shape of its oral shields, compared to the simple triangular shields of *O. brachygnatha*.

Ophiacantha yaldwyni Fell

Ophiacantha yaldwyni Fell, 1958: 23, pl. 4, figs F, H, I.

Specimens examined: 1, NMV H361, 38°24.5'S, 149°25.5'E, off Pt Hicks Vic., 823 m, coral rock 21.xi.1973; 2, NMNZ 2658, 42°29'S, 173°37'E, Kaikoura Canyon, N.Z., 1097–1006 m, 18.iii.1976.

Remarks: This species was previously known from a single specimen taken in Cook Strait, N.Z., at 1005 m (Fell 1958), and the Victorian record is thus new for Australia. The specimens are slightly smaller (6–9 mm d.d.), but agree very closely with Fell's description. Fell recorded an absence of tentacle scales after the fourth arm segment in the holotype; the present material does not conform in that respect, the tentacle scales persist along most of the arms as thin spikes with three terminal thorns. *O. yaldwyni* is otherwise characterized by a disc cover of evenly spaced thorny granules, six robust arm spines with asymmetric and largely terminal thorns, 5–9 irregularly arranged, club-shaped oral papillae, and rhomboidal oral shields. The type specimen cannot be located and is feared lost.

Key to southern Australian species of *Ophiacantha**

1. Disc covered dorsally by slender, multilid spinelets 2
Disc covered dorsally by granules or spinules 3
2. Dorsal arm plates triangular; longest armspines clavate *O. clavipera*
Dorsal arm plates bell-shaped; longest armspines evenly tapered *O. brachygnatha*
3. Disc covered dorsally by granules 4
Disc covered dorsally by spinules 5

4. Disc granules as wide or wider than high, blunt; first uppermost armspine enlarged *O. shepherdi*
Disc granules as high or higher than wide, with terminal thorns, uppermost armspines of similar size *O. yaldwyni*

5. Disc with pointed spinules, enlarged inter-radially near disc margin; arm spines alternating in number *O. alternata*
Disc with pointed spinules enlarged near disc centre; armspines not alternating in number *O. heterotyla*

Ophioprium rosea (Lyman) n. comb.

Ophiacantha rosea Lyman, 1879: 139, pl. X, figs 267, 268; 1882: 184, pl. 25, figs 10, 11.—Fell, 1958: 23, pl. 4, figs J, K.—McKnight, 1967: 308.

Ophiacantha truncata Koehler, (1930: 62, pl. VI, figs 13–14.

Specimens examined: Holotype, BM(NH) 82.12.23.175, 50°10'S, 74°42'W, S Indian Ocean, 320 m, S.I.1876 (Challenger Stn 308); 11, NMV H364 & 1, NMNZ 2654, 39°44.5'S, 148°49'E, Bass Strait, 640 m, 24.xi.1973; 2, NMNZ 2655, 43°14'S, 173°39'E, Pegasus Bay, N.Z., 1006–512 m, 27.ix.1976; 1, ZMC, 38°15'S, 149°20'E, S of Cape Everard, Vic., 270–470 m, 19.ix.1914 (holotype of *Ophiacantha truncata* Koehler).

Remarks: This robust, brightly coloured species has been recorded from New Zealand by Fell (1958) and McKnight (1967), and southern Chile, Japan, and Crozet Is. by Lyman (1879, 1882), thus its occurrence in Australian waters is not unexpected.

The new material ranges 7–15 mm d.d., and has arms about 4 × d.d. At their bases, the arms of a 12 mm d.d. specimen are 4 mm high and 3 mm wide, with 10 arm spines up to 4 mm long. The arms therefore have a very robust appearance. The disc is covered entirely with small thorny stumps up to 3 × higher than wide. There are 18 oral papillae on each jaw, 6 internal and the remainder external on each side. The internal papillae are rather spini-

* Other species recorded from southern Australian waters and referred to *Ophiacantha* by H. L. Clark (1946) are here regarded as belonging to different genera, viz: *Ophiacantha truncata* = *Ophioprium rosea* (Lyman); *Ophiacantha fidelis* = *Ophiomitrella fidelis* Koehler; *Ophiacantha congesta* = *Ophialcaea congesta* (Koehler); *Ophiacantha valenciennesi* = *Ophiotreta valenciennesi* (Lyman).

form, whereas the external ones are spatulate. The oral shield is of an unusual bell-shape, with the apex of the bell pointing distally. There is one very large paddle-shaped tentacle scale on each pore except the first, where there are occasionally two (as in the holotype).

The concealed radial shields, numerous oral papillae generally of two distinct types and position, two basal tentacle scales, and following single scale of very large size, indicate that this species should be placed in *Ophioprium* H. L. Clark rather than *Ophiacantha*. In other respects, such as size, form and sculpturing of arm spines, and the nature of the arm plates, *O. rosea* closely resembles the two large species of *Ophioprium* (*O. larissae* and *O. kapalae*) known from the Tasman Sea (Baker 1979). *O. rosea* is distinguished by its red colour, short arms, and the shape of its oral shields and tentacle scales.

Ophiacantha truncata Knebler, known from two specimens from just northeast of Tasmania, is here regarded as a junior synonym of *O. rosea*. The holotype has identical disc stumps, arm spines, arm plates, and oral shields, and up to 17 oral papillae of two kinds. The five arm bases have only one large tentacle scale to each pore indicating that the presence of more than one scale is not a stable character.

Ophioplinthaca Verrill, 1899

Ophioplinthaca incisa (Lyman)

Ophiomitra incisa Lyman, 1883: 263, pl. VI, figs 89, 90.

Ophioplinthaca incisa Verrill, 1899: 351.—H. L. Clark, 1915: 211.

Specimens examined: 8, NMV H361, 38°24.5'S, 149°25.5'E, S of Pt Hicks, Vic., 823 m, rock and coral, 21.xi.1973.

Remarks: The discovery of this species in the waters of southern Australia is somewhat surprising considering that all previous records have been from western Atlantic Ocean near Barbados and Dominica. Its bathymetric range of 610–1572 m, suggests however, that it may well be widespread like some other deep continental slope ophiuroids.

The largest specimen is 17 mm d.d., and one has what is possibly a dwarf male attached to its aboral surface. The specimens match Lyman's description closely, and the range of sizes shows small variations: the arm spines vary from five to seven, and the disc cover

varies from smooth stumps at the edge to thorny stumps near the disc centre.

Ophioplinthaca is cosmopolitan on the continental shelf or deeper, and contains about 30 nominal species. No representative has hitherto been recorded from Australia, although several are known from Indonesian waters (Koehler 1930). Of those, *O. vicina* Koehler from the Banda Sea, 1595 m, is very close to this species. It is known from a single specimen, and appears to differ mainly in the shape of the oral shields and the alignment of the external oral papillae.

FAMILY Ophiactidae

Ophiactis Lütken, 1856

Ophiactis tricolor H. L. Clark

FIGS 33, 34

Ophiactis tricolor H. L. Clark, 1928: 427–428, Fig. 126; 1938: 262; 1946: 208.—A. M. Clark, 1966: 326 (in key).

Ophiactis laevis H. L. Clark, 1938: 268–270; 1946: 208.

Ophiactis luetkeni Koehler, 1907: 245.

Specimens examined: Holotype SAM K213, no locality data or depth; paratype SAM K214, no locality data or depth (Figs 33, 34); 2, NMNZ 2079, 3 km off West Beach, Gulf St Vincent, S.A., 9 m, 8.vi.1968; 2 NMNZ 2083, off Pt Madsden, S.A., 20 m, Jan. 1965; 1, NMNZ 2081, Yankalilla Bay, S.A., 18 m, no date; 1, NMNZ 2078, West Id, S.A., 2 m, 20.x.1967; 1, NMNZ 2082, wreck of *Norma*, Gulf St. Vincent, S.A., 12 m, 1.i.1965; 2, BPBM W1806, Investigator Strait, S.A., 30 m, no date; 2, BPBM W1809, Investigator Strait, 43 m, no date; 3, BPBM W1825 off Glenelg, Gulf St Vincent, S.A., 12 m, rock, among sponges, no date; 2, paratypes of *O. laevis* WAM 221/2–39, Bunbury, W.A., 26.x.1929, no depth; 2, WAM 499–74 SW of Bunbury, W.A., 20 m, 13.iv.1963; 4, NMNZ 2069, Eagle Bay, Cape Naturaliste, W.A., 1–5 m, 24.ii.1975; 1, NMNZ 1838, Yallingup, W.A., 1–3 m, 22.ii.1975; 1, MNB 4549, Geraldton, W.A., no depth; 1, ZMH 25444, Fremantle, Gage Roads, W.A., 7–18 m, 4.v.1905; 1, WAM 319–78, W side Goss Passage, Abrolhos Is, W.A., 33–35 m, no date.

Remarks: *Ophiactis tricolor* was described by H. L. Clark from Sir Joseph Verno's collections dredged in Gulf St Vincent and Spencer Gulf, South Australia. Clark (1938) mentioned a specimen of *tricolor* in the "Melbourne Museum" collected in 40 fathoms north of Cape Borda, Kangaroo Id, S.A. but there appear to be no subsequent records of this species in the literature. The new records listed

here show it to be distinctly southern and southwestern Australia in distribution.

H. L. Clark (1938) reported a second and new species, *O. laevis*, from dredged samples in Koombana Bay (Bunbury), and Dongarra, Western Australia, and provisionally attributed two specimens (MNB 4549 & ZMH E5444) from Fremantle and Geraldton (reported by Kochler 1907 as *O. leutkeni*) to his new species. Clark (1946, p. 207) separated *O. laevis* from *O. tricolor* by differences in the size of the disc scales, and radial shields, as well as by colour as follows:

<i>O. laevis</i>	<i>O. tricolor</i>
1. disc with smooth coat of small rounded scales.	disc scales larger and less smooth.
2. radial shields very small, not much larger than some of disc scales.	radial shields considerably larger.
3. disc usually purplish-rose arms variegated but not banded.	disc grayish or dirty yellowish, arms normally banded with pinkish white, rosy red, and dull blue.

Both species were characterized in Clark's key by: (a) a quite large single oral papilla, (b) radial shields small, less than .25 disc diameter, (c) very small and numerous disc scales.

The series of specimens available has shown that the small differences used by Clark to separate *laevis* from *tricolor* can be attributed to normal variation within the one species. Consequently, *O. laevis* is here synonymized with *O. tricolor*.

FAMILY Amphiuridae

Amphiura elandiformis A. M. Clark

Amphiura elandiformis A. M. Clark, 1966: 331, fig. 6 f-l; Dartnall, 1980: 40, fig. 13.

Specimens examined: 3, NMNZ 1853, 43°00'S, 148°13.6'E, off Eaglehawk Neck, Tas., 122 m, 13.iii.1973; 1, NMNZ 2615, off Burnie, Tas., 20 m, 6.ii.1970; 1, NMNZ 2616, Great Taylor Bay, Bruny Id, Tas., 14.ii.1972.

Remarks: This species was previously known only from Pt Phillip, Victoria, and with its discovery in eastern Tasmanian waters, it may be expected along the entire southern Australian coast. The specimens range 5-7 mm d.d., and confirm the distinctive features of this amphiuroid: the disc is petaloid and covered above with

small scales, and below with naked skin. The radial shields are long (2.3 mm on the 7 mm specimen), narrow, and bowed. The distal oral papilla is wide and rounded, there are two tentacle scales on each pore, and the second to lowest arm spine has a proximally-directed hyaline hook or is bihamulate.

Amphiura elandiformis is similar to two other southern Australian amphiuroids, *A. dolin* and *A. multiremula* (both of H. L. Clark) and one New Zealand species, *A. correcta* Kochler, but they can be distinguished by different combinations of the above features.

Amphiura multiremula H. L. Clark

Amphiura multiremula H. L. Clark, 1938: 228.-A. M. Clark, 1966: 336, fig. 7a-c.

Specimens examined: 1, NMNZ 2617, West Id, S.A., 2 m, 29.i.1975; 1, NMNZ 2618, Eagle Bay, W.A., 1 m, 24.ii.1975.

Remarks: This amphiuroid was hitherto known only from 3 Port Jackson and Long Reef, N.S.W. specimens. The present specimens are 4.0 and 5.5 mm d.d., and the largest has 9 arm spines. This large number of arm spines, and their flat, blunt shape, help to characterize this species, which is otherwise distinguished from the many other Australian congeners by very fine, complete disc scaling, small radial shields (0.2-0.33 d.d.), and oral shields with a semi-circular proximal border.

The holotype of *A. multiremula* has been figured by A. M. Clark (1966).

Amphiura magellanica Ljungman

Amphiura magellanica Ljungman, 1867: 320.-Mortensen, 1924: 132, fig. 14.

Specimens examined: 2, NMNZ 2620, S of Warrnambool, Vic., 220-310 m, 14.v.1969.

Remarks: This species is apparently circumpolar in subantarctic and cold temperate latitudes, having been recorded from the south Atlantic Ocean, Patagonia, southern New Zealand and, now, southern Australia.

The two Warrnambool specimens measure 2.4 and 3.7 mm d.d. They show the characteristic lengthening of the lowermost of the 7 arm spines, and the large leaf-shaped distal oral papilla and tentacle scales. *Amphiura magellanica* is viviparous and hermaphroditic—features which separate the species from the similar *A. spinipex* Mortensen from New Zealand.

Amphiura trisacantha H. L. Clark

FLOS 43-48

Amphiura trisacantha H. L. Clark, 1928: 425, figs 125 a & b.

Specimens examined: Holotype, SAM K212, Spencer or St Vincent Gulfs, S.A., no depth or date; 1, NMNZ 2073, Upper Spencer Gulf, S.A., 9 m, 11.ix.1973; 1, NMNZ 2619, North Arm, Westernport, Vic., 4 m, 13.vi.1976.

Remarks: This species was hitherto known only from the holotype. The new material measures 2.5 and 6.5 mm d.d., and although all the arms are broken, fragments with the largest specimen indicate arms 4–5 \times d.d. The arm spines number 5 at the arm bases, and reduce to 3 within six segments. The uppermost spines are pointed and slightly flattened, and the longer lowermost spines are more circular in cross section, and evenly tapered to a sharp point.

In other respects the specimens are in close agreement with the holotype and Clark's description. Clark's photograph of the holotype does not illustrate the species adequately, and we therefore provide camera lucida drawings of the now damaged type specimen (Figs 45–48) and the one from Upper Spencer Gulf (Figs 43 & 44).

FAMILY Ophiotrichidae

Ophiotrix Müller & Troschel, 1840

Ophiotrix (*Placophiotrix*) *albostriata* H. L. Clark

FIGS 49–54

Ophiotrix albostriata H. L. Clark, 1928: 429, fig. 127.

Placophiotrix albostriata H. L. Clark, 1946: 227.

Ophiotrix (*Placophiotrix*) *albostriata* A. M. Clark, 1967: 648.

Specimen examined: Holotype SAM K215, Great Australian Bight, no depth or date.

Remarks: This holotype (d.d. 10 mm) remains the only known specimen and we give here drawings of various parts of it to supplement Clark's description and figure. The specimen is now very faded, but two parallel lines are visible on both dorsal and ventral surfaces of the arms after about the 20th segment. This species is similar to *O. (Placophiotrix) spongicola* in general appearance, but differs in the shape of its dorsal arm plates and oral shields. The disc cover and overall colour pattern were stressed by H. L. Clark as being definitive, but in our experience, the variation in these features shown by *O. (Placophiotrix) spongicola* encompasses those in *albostriata*. The disc cover of *O. albostriata* is also like that of *O. (Placophiotrix) lineocerulea* H. L. Clark

(holotype SAM K218) (Figs 55–59). The dorsal and ventral arm plates (Figs 52–54, 57 & 58) are, however, quite distinct in these two species, and *O. lineocerulea* is known only from northern and eastern Australia, from Broome to Moreton Bay.

Ophiotrix (*Keystonea*) *hymenacantha* H. L. Clark

FIGS 60–62

Ophiotrix hymenacantha H. L. Clark, 1928: 431, fig. 128.

Ophiotrichoides hymenacantha H. L. Clark, 1946: 233.

Ophiotrix (*Keystonea*) *hymenacantha* A. M. Clark, 1967: 648.

Specimen examined: Holotype, SAM K217, Great Australian Bight, no depth or date.

Remarks: This species is known only from the 8 mm holotype. H. L. Clark (1946) inferred that the specimen might be from the north-western coast of Australia, rather than the Bight, but there is no information on the label to suggest this, and in the absence of new material we must assume it is a southern form. There are of course other "northern" ophiroids in the Great Australian Bight and South Australian gulfs (e.g. *Astroboa ernae* Döderlein & *Amphiplopus ochroleuca* (Brock)), and it may well be that if this is a representative of the tropical subgenus *Keystonea*, it has evolved in the relative isolation of the southern region.

In many ways, however, *hymenacantha* reminds us of an aberrant *O. (Placophiotrix) spongicola*—it has the same shaped arm spines, arm plates, and oral shields, and we have seen *spongicola* specimens with a naked dorsal disc surface. We have as well encountered webbed arm spines in small specimens of the several hundred *spongicola* examined: Up to a d.d. of 3 mm, specimens of *O. spongicola* from the Abrolhos Is. W.A., and Investigator Strait, S.A., reveal, on segments under the disc, proximal arm spine webbing, as well as upper arm plates with scattered low thorny stumps. Larger specimens, however, lack these apparent juvenile characters. In view of that last fact, and the very distinctive colour pattern of *O. spongicola* (see Baker 1981), we consider that the colourless, enigmatic *O. hymenacantha* should be retained in the subgenus *Keystonea* by virtue of its naked upper disc surface, at least until a growth series is found which indicates another relationship. Figures 60–62 show diagnostic features of the type specimen.

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THE CONCEPT OF AN 'EDIACARAN' PERIOD AND ITS STRATIGRAPHIC SIGNIFICANCE IN AUSTRALIA

BY R. J. F. JENKINS

Summary

A 20 year cycle of ideas has led to a concept of an 'Ediacaran Period' embracing the geological time interval characterized by the soft-bodied metazoan assemblages of the terminal Precambrian. Continuing finds of such assemblages emphasize their potential value for biostratigraphy. Geochronological studies suggest that the earliest finds may be at about 640-620Ma; metazoans appear to have become diverse and relatively numerous during the interval 600-570 Ma. Evidence from central England establishes that the Ediacaran does not overlap the Cambrian and that separate sequential depositional events represent these time intervals. The Ediacaran is Precambrian in aspect, without the significant skeletal-bioclastic component typifying the Palaeozoic or Phanerozoic. Studies of Harland & Herod (1975) and Glaessner (1977, 1979b) link the Ediacaran with the post-glacial part of the Proterozoic Adelaidean succession, and by implication indicate a type area within the Flinders Ranges, South Australia. A stratotype for the Ediacaran is nominated at Bunyeroo Gorge, and comprises the Wonoka Formation and Pound Subgroup, the age of the Wonoka Formation being suggested to approximate the time of appearance of megascopic metazoans. The exposure of the Rawnsley Quartzite of the Pound Subgroup in Bunyeroo Gorge is made the stratotype of a Late Ediacaran Epoch reflecting the major evolutionary radiation of surviving invertebrate phyla.

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by R. I. F. JENKINS*

Summary

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A 20 year cycle of ideas has led to a concept of an 'Ediacaran Period' embracing the geological time interval characterized by the soft-bodied metazoan assemblages of the terminal Precambrian. Continuing finds of such assemblages emphasize their potential value for biostratigraphy. Geochronological studies suggest that the earliest finds may be at about 640-620 Ma; metazoans appear to have become diverse and relatively numerous during the interval 600-570 Ma. Evidence from central England establishes that the Ediacaran does not overlap the Cambrian and that separate sequential depositional events represent these time intervals. The Ediacaran is Precambrian in aspect, without the significant skeletal-bioelastic component typifying the Palaeozoic or Phanerozoic. Studies of Harland & Herod (1975) and Glaessner (1977, 1979b) link the Ediacaran with the post-glacial part of the Proterozoic Adelaidean succession, and by implication indicate a type area within the Flinders Ranges, South Australia. A stratotype for the Ediacaran is nominated at Bunyerroo Gorge, and comprises the Wonoka Formation and Pound Subgroup, the age of the Wonoka Formation being suggested to approximate the time of appearance of megascopic metazoans. The exposure of the Rawnsley Quartzite of the Pound Subgroup in Bunyerroo Gorge is made the stratotype of a Late Ediacaran Epoch reflecting the major evolutionary radiation of surviving invertebrate phyla.

Introduction

Glaessner (1959) compared finds of early soft-bodied metazoans at Ediacara, South Australia, with similar fossil remains from Charnwood Forest, Leicestershire, England, and the Nama Group of Namibia (South West Africa), and established the age of these assemblages as late Precambrian. These finds are now justifiably famous and the known record of comparable fossil remains is becoming increasingly extensive with some 18 or so occurrences widely sited about the globe (e.g. Glaessner 1979b, fig. 2). Though the organisms often attained large size and show a general lack of hard parts, their fossil imprints show no evidence of macrophagous predation, and this, coupled with rapid burial, was of undoubted importance for their preservation (Wade 1968; Glaessner 1979b). The kinds of organisms represented include medusoid coelenterates, a member of the conulata, chondrophore hydrozoans, representatives of sea-pen-like animals, several kinds of worms, primitive arthropods and the problematic lophophorate *Tribrachidium* Glaessner. Other curious sack-shaped organisms and enigmatic forms composed of chambered vanes are referable to the new Phylum *Petalonamae* Pillug.

Amongst students of these fossils there is broad consensus that the remains reflect a phase of accelerated animal evolution preceding the Cambrian (Glaessner 1961, 1971, 1972, 1977, 1979a,b; Glaessner & Walter 1981; Cloud 1976a,b; Sokolov 1976a,b, 1977; Stanley 1976a,b; Sepkoski 1978, 1979; Ford 1979, 1980b; Lowenstam 1980). The interval during which these organisms lived is variably recognized by Western workers as the "Ediacarien" Stage (Termier & Termier 1960) or as either the Ediacarian (Cloud 1972, 1976a,b) or Ediacaran Period (Harland & Herod 1975; Glaessner 1977, 1979b). The approximately equivalent interval is generally termed Vendian by the Soviets (e.g. Sokolov 1973; Keller 1979). The broad relationship between the Ediacaran and Vendian is indicated in Glaessner (1979b, fig. 1).

Of recent years, diverse new assemblages of Ediacaran fossils have been located in northern Russia in parts of the Redkino substage of the Valdai Group, on the Onega Peninsula and the Zimniy Bereg (Winter Coast) of the White Sea (Keller & Fedonkin 1977, 1978, 1980a, 1981). As well as these having several taxa in common, some 10 or 11 species which variably occur in these assemblages are also present at Ediacara and other fossil sites in the Flinders Ranges, South Australia (Fig. 1). This finding led Keller & Fedonkin (1976)

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Fig. 1. Ediacaran localities discussed in text. Larger map shows greater part of Flinders Ranges with outcrop of Pound Subgroup indicated by areas of stipple. Occurrences of Ediacara assemblage are marked 'F'. New occurrences are from work of Mr Colin Ford, Mr Jim Gehling and Dr Brian Daily. Base map after Jenkins & Gehling (1978).

and Fedonkin (1977, 1981) to suggest that the northern Russian sites and the localities in the Flinders Ranges are closely equivalent in time. Several of the shared taxa have been considered as constituting an Oppel zone (Rozanov & Sokolov 1980). A number of other pairs of sites share either one or more species or have taxa showing resemblances suggestive of an evolutionary affinity. "Medus-

oids" are virtually ubiquitous. Thus it is apparent that all the finds are broadly related in geological time, and it becomes appropriate to consider the potential use of Ediacaran fossils as a means of correlating between major land areas.

The recognition of such a biostratigraphy necessitates the nomination of stratotypes for the time divisions involved. Time-rock divisions such as the Sinian System (Grabau 1922) erected for sequences in northeastern China (standard section in Ji Xian County, Tianjin, Kao *et al.* 1934) and extended by Lea & Chao (1924) to sections in the Yangtze Gorges, Hubei Province, South China, or the Marinoan 'Series' (Mawson & Sprigg 1950), measured on rocks cropping out immediately south of Adelaide, South Australia (Thomson 1966), have useful regional application for purposes of intracratonic correlation. The modern usage of the Marinoan in this sense is discussed by Thomson (1964, 1969). Historically, these divisions have priority over subsequently designated time-rock terms. However, the intervals of time embraced by them are incomplete or rather broad and their correlation between different land areas remains essentially arbitrary.

Current usage of the Vendian is subject to controversy as to its stratigraphic beginning (Keller 1979). As yet no stratotype has been nominated for the Ediacaran, which however, is linked geographically with the Flinders Ranges in name and in its associated assemblage. This paper attempts to order geological and evolutionary events in the terminal Precambrian and examines potential stratotypes for the Ediacaran.

Concept of an Ediacaran Period

Termier & Termier's (1960) erection of an "Ediacarien" Stage met with little support, the fossil remains being known essentially at only three world localities at that time. In a later work the same authors (Termier & Termier 1967, p. 141) discuss "la faune d'Ediacara", and subsequently they refer to the different world occurrences of the comparable fossils as "la faune ediacarienne" or "des faunes ediacariennes" (Termier & Termier 1968, p. 74 & 76). Wade's (1970) notation of an "Ediacara fauna" was widely adopted and used informally to designate assemblages from a then increasing number of localities reviewed by Glaessner (1971). The tacit implication of this terminology was that the fossils from

different areas showed similarities and were of comparable age, that is, late Precambrian.

The concept of an "Ediacarian" Period to embrace the rocks containing these early soft-bodied metazoan assemblages was advanced by Cloud (1972, 1973, 1976a,b) who also reviewed the contentious question as to the relationship between this interval and the succeeding Cambrian, characterised principally by shelly fossils. Cloud (1976a,b) made several proposals concerning either the maintenance of the "traditional" Cambrian boundary, or its lowering to include the Ediacaran, a possibility also explored by other authors (e.g. Frey & Seilacher 1980; Rozanov & Sokolov 1980). Cloud further advanced the notion that the etymology of the divisions Phanerozoic and Palaeozoic were such that these time terms should properly be considered as extending downwards to the start of his "Ediacarian".

Harland & Herod (1975) nominated an Ediacaran Period bounded by suggested age limits of $7650 \pm$ and $2570 \pm$ Ma and indicated to comprise the latest part of the Adelaidean, the time term used (Thomson 1969) to embrace the depositional history of the cumulatively measured 24 km or so of Precambrian sediments occurring in the Adelaide Fold-Belt (Geosyncline). Harland & Herod placed the Ediacaran in a sequential division of time intervals from oldest to youngest respectively: Sturtian, Varangian, Ediacaran and Cambrian. The Sturtian (Howchin 1918, p. 346; Mawson & Sprigg 1950) is the time division associated with the earlier and major phases of glaciation in the Adelaidean. The Varangian is associated with late ice activity in the Precambrian (Harland 1968), and in the usage of Harland & Herod (1975) it is implicitly equated with the Marinoan phase of glaciogenic deposition in the Adelaidean. This, the Elatina glaciation (Mawson 1949), is represented by diamictites and varvites included within the Elatina Formation, at the top of the Umberatana Group, in the Flinders Ranges. Glaessner (1977, 1979b) maintains a comparable division of the late Precambrian to that of Harland & Herod and in his reviews of pertinent geochronological data, indicates that rocks with Ediacaran assemblages tend to fall in the age range 640–575 million years. He further cautions that the "appropriate datings . . . do not support any biostratigraphic subdivision at the present state of our knowledge".

However, workers such as Sepkoski (1978, 1979) and Brasier (1979) extend the studies of Soviet students such as Sokolov (1973, 1976a) and recognise informal subdivisions within the Vendian. In the work of Sepkoski (1978, 1979) the Vendian is approximated with Cloud's (1972, 1976a,b) usage of the "Ediacarian" and is subdivided into an informal four fold division of major biotic units, though it is admitted that current biostratigraphic control does not permit accurate correlations. Other Soviet reviews of the Vendian (Sokolov 1976b, 1977; Yakobson & Krylov 1977; Keller 1979) suggest that these divisions reflect an oversimplification. On the Russian Platform, Ediacaran fossils occur within the Valdai Group which Keller (1979) recognizes as the Vendian *sensu stricto*. Keller (1979) considers that "there are no reliable radiometric data for dating the Vendian lower boundary" and suggests that a previously accepted c. 680–650 Ma K-Ar glauconite date for the Vendian basement must be corrected. On the basis of newer dates he considers that the base of the Valdai Group is about 620–600 million years old.

The preceding short review indicates that in the literature the Ediacaran has been attributed varying status. These philosophical viewpoints may be summarized as follows:

1. A majority of studies equate the Ediacaran with soft-bodied assemblages of sub-Cambrian metazoans which have been broadly termed the Ediacara fauna. Glaessner (1977, 1979b) indicates that the rocks containing these remains fall into the approximate age range of 640–570 Ma.
2. A minority of students attribute to the Ediacaran the significance of a biostratigraphic stage, or suggest that at least in part it constitutes an assemblage zone.
3. A majority of studies imply or indicate that the Ediacaran is Precambrian, and representing the latest part of that Erathem.
4. A minority of authors consider either that the Ediacaran validly comprises part of the Cambrian or that the lower boundary of the Cambrian should be extended downwards to embrace the Ediacaran.
5. A minority of students imply that the Ediacaran is of Phanerozoic and Palaeozoic aspect and advocate its inclusion within these divisions.

6. Several workers (Harland & Herod 1975; Glaessner 1979b) attribute the Ediacaran time-rock status, indicating it to represent a part of the Upper Proterozoic and a division of the Adelaidean, thereby nominally restricting its type-area to the Adelaide Fold-Belt. By implication, the lower boundary of the Ediacaran lies above the Marinoan glaciogenic event recognized in this region.

7. Some recognise informal divisions within the Ediacaran, these divisions variably numbering between two and four.

8. A close equivalence is recognized between the Ediacaran and Vendian.

Discussion

General

As the Ediacaran has been attributed several different philosophical meanings the fairest approach in attempting to nominate a stratotype might be to choose a section which best illustrates concepts held by the majority of earlier students. This approach does not imply direct maintenance of priority. Certainly those students who attribute a time-rock meaning to the term (Harland & Herod 1975; Glaessner 1977, 1979b) come closest to providing an adequate definition. The second and major requirement of the stratotype is that it should encompass or be bounded by distinctive geological phenomena which provide the greatest potential for correlation, and consistent with the broader interpretation of the nominate division.

The idea that the Ediacaran can be considered as a short downwards extension of the Lower Cambrian is not supported by geochronological data. A U-Pb zircon-date (concordia upper intercept model) of 620 ± 20 Ma (Glover & Shih 1973) for a felsic tuff-breccia in near association with worm-like impressions from North Carolina (Cloud *et al.* 1976) is perhaps the oldest well founded age linked with any of the Ediacaran fossils. Older datings have been well publicised (see reviews of Glaessner 1977, 1979b) but are not closely consistent with those obtaining for the majority of finds.

The first Ediacaran assemblage actually discovered (Gillrich 1929, 1933; Germs 1972, 1974) occurs in the lower part of the Nama Group in Namibia. The Nama Group is placed in stratigraphic perspective by Kröner (1977) and formally subdivided by Kröner

et al. (1980). Kröner *et al.* (1980) indicate that in part the Nama Group rests unconformably on a sequence containing volcanic rocks which give a possible metamorphic resetting age of 686 ± 32 Ma; elsewhere the Nama is intruded by granitoid rocks dated at 553 ± 13 Ma (Rb-Sr whole rock isochron ages; Allsopp *et al.* 1979; decay constants of Steiner & Jäger 1977). Rb-Sr dating of shales in the lower Nama Group confirms a late Precambrian age and Kröner (1977) brackets the Kuibis Subgroup, the earliest part of the Nama and major fossiliferous interval, between c. 607* and c. 636* million years (*superscript indicates correction of data to constants of Steiner & Jäger 1977). Reviews of age data in preparation by the writer suggest younger ages for other Western occurrences of Ediacaran fossils. The possible lower age of 620–600 Ma for Soviet occurrences (Keller 1979) has already been mentioned.

In their assessment of age data relating to the Ediacaran and Cambrian, Cowie & Cribb (1978) find that the base of the Cambrian may be bracketed between 590 and 560 Ma. Kröner *et al.* (1980) suggest that the base of the Cambrian be recognized at 560 Ma. An increasing body of new radiometric data from England suggests that this boundary may actually be younger again. In central western England, Early Cambrian strata of the "Non-Trilobite" Zone and the "Olenellid" Zone rest unconformably on metamorphosed rocks dated by Rb-Sr studies at 536 ± 8 Ma, with related granophyric intrusion at 533 ± 13 Ma (Patchett *et al.* 1980 & included references). A similar Rb-Sr isochron age of $540* \pm 58$ Ma was obtained by Cribb (1975) from diorites intruding the southern part of the Charnian Complex. The Early Cambrian Hartshill Formation lies unconformably above a comparable diorite and the upper part of this Formation contains a shelly assemblage considered equivalent to the *Dokidocyathus regularis* zone of the Siberian Tommotian (Brasier *et al.* 1978; Brasier & Hewitt 1979); elements of the lowest Tommotian zone are also present "although largely reworked" (Brasier *et al.* 1978). Further work on the dating of the sub-Cambrian of England is proceeding (Beckinsale *et al.* 1981).

The geochronological data just reviewed continue to support Glaessner's (1977, 1979b) finding that rocks with characteristic Ediacaran metazoans may occur as early as c. 640

Ma. However, the few items of data fall about a mean of c. 620 Ma, which may be a slightly firmer age for the earliest known metazoans. The termination of the Ediacaran may lie at c. 560 Ma or possibly as young as c. 530 Ma. These estimates indicate a possible maximum duration of c. 110 Ma for the deposition of rocks with Ediacaran metazoans, and a minimum duration of c. 60 Ma. Either of these estimates are comparable with the likely duration of 55 to 95 Ma for the 'traditional' Cambrian (based on data of Cowie & Cribb 1978) and indicate that in a hierarchy of geological time divisions the Ediacaran and Cambrian must be accorded equal status.

The occurrence of a reasonably diverse Ediacaran assemblage is well documented in the middle part of the Charnian, or the Wondhouse Beds of the Maplewell Group (Ford 1958, 1980a; Brasier *et al.* 1979). However following deposition of the Charnian succession, folding, metamorphism, intrusion and deep erosion occurred *prior* to a new transgressive event heralding the start of the Early Cambrian (Brasier 1979, 1980; Brasier & Hewitt 1979). Any estimate of the duration of this sub-Cambrian orogenic event and the subsequent cycle of uplift and erosion must be speculative, but an interval of 10 to 15 Ma is reasonable. This tectonic punctuation between the deposition of rocks with Ediacaran fossils and true Cambrian sediments, which can be recognizably dated biostratigraphically as Tommotian (Brasier *et al.* 1978), establishes beyond reasonable doubt that the time interval represented by Ediacaran sediments and the time of Cambrian deposits are two quite separate geological cycles sequential in Earth history. This finding is also supported by the stratigraphy of the Adelaide Fold-Belt.

I am not in agreement with Cloud (1973, 1976a,b) that the etymology of the names Phanerozoic and Palaeozoic provides an initial grounds to alter the traditional beginning of these time intervals and extend them earlier to include the Ediacaran. The comparatively rare Ediacaran metazoan remains occur in rocks which are otherwise little different from those of earlier times in the Proterozoic. In contrast, sediments of the Early Cambrian transgression (Daily 1972; Brasier 1979, 1980) suggest a filling of the seas by invertebrates, with frequent bioturbation (Brasier & Hewitt 1979; Frey & Seilacher 1980; Fedonkin 1981) and an increasing content of metazoan

skeletal debris, which in conjunction with calcareous higher algae, forms extensive biogenic limestones. Comparable characteristics typify the remaining Palaeozoic, with skeletal limestones and reefal deposits abundant. These epochal skeletal and lithic changes which are closely related in time to the base of the 'traditional' Cambrian are surely of greater significance for stratigraphy and historical geology than the sporadic and fragmentary earlier record of soft-bodied animals, intriguing though this may be for our knowledge of evolution. Thus there are good geological reasons for considering that the Ediacaran is properly part of the Precambrian, and its significance for evolutionary studies is that it contains the Precambrian precursors of major phyla which only later provide the spectacular skeletal record characteristic of the Palaeozoic and the Phanerozoic as a whole.

Biostratigraphy

Virtually all published concepts of the Ediacaran embrace the unique, large, soft-bodied metazoan remains which are found in its rocks. In this sense, the Ediacaran is essentially a biostratigraphic concept with similar fossils in different areas suggesting an approximate equivalence in time. Any realistic stratotype should reflect this biostratigraphic aspect as it potentially provides a primary framework for correlation.

The Ediacaran assemblages at the various known-world sites are not uniform in composition and Glaessner (1977) remarked on this in relation to the usage of term 'Ediacara fauna'. Jenkins & Gehling (1978) suggested that the remains of the organisms preserved probably represent only part of the original life community, the barrier to the preservation of small organisms effectively being the grain-size of the enveloping sediment (cf. Glaessner (1972). Instead Jenkins & Gehling prefer to name the incomplete preserved community the 'Ediacara assemblage'. This usage is only of strict relevance to the remains from the Flinders Ranges or type area. Assemblages from other geographic localities should be identified by an appropriate site or stratigraphic designation; i.e. the 'Nama assemblage' from Namibia or the 'Charnian assemblage' from England.

The Ediacara assemblage *sensu stricto* is now well documented (Glaessner & Daily 1959; Glaessner & Wade 1966; Glaessner 1980) but the description of the other occur-

rences is not uniform. Fedonkin (1977, 1981) is extremely active in the Soviet sphere and various other studies are proceeding. Enough information is now available to suggest that the metazoan remains can be divided into two broad groups.

One group embraces the remains from the lower Nama Group, the Charnian, and the fossils which Anderson & Misra (1968), Misra (1969, 1971) and Anderson (1972) documented from the Conception Group on the Avalon Peninsula of Newfoundland. The Nama assemblage contains the distinctive fossils *Rangia* Gülich, *Pteridinium* Gülich and *Erniella* Pflug and new reviews of these enigmatic remains are being prepared by the writer. Preliminary remarks concerning a revised structural interpretation of the sack-shaped *Erniella* are given by Jenkins *et al.* (1981). *Pteridinium* and *Erniella* represent organisms with a unique structural organization which qualifies their recognition as a new phylum, the Petalonamae Pflug. The Nama Group contains the only known world occurrence of *Pteridinium simplex* Gülich. The structure of *Rangia* is quite separate to that of the Petalonamae, but closely similar to as yet undescribed fossils from the Charnian and Newfoundland assemblages, and probably to *Charnia* Ford, which is common to both these areas. These organisms comprise an extinct order of primitive anthozoan coelenterates, and their complex, ramifying structure suggests specialized adaptation to suspension feeding with extreme "scavenging" capacity. It might be inferred that at this time either the plankton, or algal or bacterial detritus was rare, an interesting possibility in relation to the stratigraphic proximity of glaciogenic deposits in the Nama Group, and the potential inferences this has to the climate. Age data relating to these assemblages (review in preparation) suggest a bracketing between c. 640–620 Ma and c. 600–590 Ma. An aspect of the assemblages of this interval is that associated trace fossils are limited in diversity or comparatively uncommon. The evolution and radiation of the *Rangia*-like organisms and the Petalonamae were evidently concomitant events and may relate to the earliest appearance of megascopic metazoans.

The second grouping comprises the better known and very diverse Ediacaran assemblage from the Flinders Ranges and now the new localities in northern Russia. The striking

characteristic of this grouping is that it includes many animals which can be more or less related to divisions and families still living in present day seas (Sokolov 1977; Fedonkin 1981). Thus there are diverse kinds of "medusoids", chondrophore hydrozoans, sea-pen-like animals, several distinctive kinds of worms, and primitive arthropods. Other problematic organisms are also present. The trace fossils of this level are diverse (Glaessner 1969, Fedonkin 1977, 1980a,b, 1981), but are restricted to markings made by creatures which moved over or burrowed horizontally in the substrate; the traces tend to show repetitive patterns reflecting behavioural adaptations towards the most efficient modes of scavenging (e.g. thigmotactic patterns). Characteristic genera of this time are forms of "*Cyclomedusa*" Sprigg, *Glaessnerina* Gerns, *Dickinsonia* Sprigg and *Tribrachidium* Glaessner. The taxon *Pteridinium venosa* Keller occurs both in northern Russia and the Flinders Ranges. The approximate age bracketing indicated for this grouping is between c. 600–590 Ma and c. 570 Ma. These remains can be considered as reflecting an initial radiation of major surviving phyla of invertebrate life (Fedonkin 1981).

The age data relating to these two groupings of assemblages are not especially significant as the reliability of the primary information is probably variable and error factors are significant. Certain geological assumptions have to be made, as well, in order to relate igneous and depositional events. Both the Newfoundland assemblage and the Charnian assemblage include *Charniodiscus* which is a frequent genus in the Flinders Ranges, and this alone suggests that the possible time separation between the two assemblage groupings is likely to be rather short. Stratigraphic evidence from the Soviet find on the Zimniy Coast (Fedonkin 1978, 1981) also suggests that the time separation between the two groupings of assemblages is short. Near the Zimniyorsk Lighthouse a 116 m thick sequence contains abundant metazoan remains in both its lowermost portion and near the top of the section. Species in the topmost part include *Cyclomedusa davidi* Sprigg, *Ovatostentum* Glaessner & Wade sp., *Dickinsonia costata* Sprigg, *D. lissa* Wade and *Tribrachidium heraldicum* Glaessner. These taxa are also present in the Flinders Ranges and are suggestive of virtual time equivalence (Fedonkin 1981). The lower part of the

Zimniyogorsk section still contains *Dickinsonia costata* and some other forms which are represented in the Flinders Ranges; these are *Pinegia stellaris* Fedonkin, *Medusinites asteroides* (Sprigg) (= *Paliella putelliformis* Fedonkin), *Protodipleurosoma rugulosum* Fedonkin, *Eidacaria flindersi* Sprigg (= *Urasiana disciformis* Pali, Fedonkin), "*Cyclo-medusar davidi*" Sprigg and *Charniodiscus* Ford sp. (= *Ramellina pennata* Fedonkin). As well, this assemblage includes well preserved examples of *Charnia masoni* Ford which has never been located in the Flinders Ranges, but is most distinctive form in the Charnian and in Newfoundland (slides made available by Dr B. Daily).

The rapid increase in diversity of life forms and coeval multiphyletic skeletalization in the Early Cambrian comprise a third metazoan radiation event which is well documented (e.g. Daily 1972, 1976; Bengtson 1977; Brasier 1979; Brasier & Hewitt 1979). This event broadly coincides with the appearance of tube constructing and tube living worms (Glaessner 1976, 1978; Føyn & Glaessner 1979). This transitional interval between the very latest Precambrian and earliest Early Cambrian may not be represented in the Adelaide Fold-Belt, where there is an unconformity of regional extent at about this level (Daily 1972, 1973, 1976). An important component of the trace fossil assemblages low in the Early Cambrian of the Flinders Ranges and also central Australia are vertical dwelling burrows like *Skolithus* Haldeman and *Monocraterion* Torell, or upright U-shaped forms such as *Arenicolites* Salter, and at a higher level, *Diplocraterion* Torell (Daily 1972, 1976; Jenkins 1975a; Gauld¹). In the light of studies by Daily and Jenkins in the areas just mentioned the trace fossil assemblage described by Webbby (1970) from the Lintiss Vale Beds in the Torowangee Group, western New South Wales, is considered to be of Cambrian aspect.

Australian occurrences of Ediacaran fossils

In the Flinders Ranges the Ediacaran assemblage is widely distributed in a thin stratigraphic interval near the base of the Rawnsley Quartzite, the uppermost formation within the Pound Subgroup (Wade 1970, Forbes 1971,

Jenkins 1975b). The stratigraphy of this major occurrence will be amplified later.

Elements of the assemblage have been reported from the northern part of the Officer Basin in the possibly late Precambrian Punkerri Beds of the Punkerri Hills, north-western South Australia (Major 1974 and references therein). Re-examination of the material suggests that some specimens are of inorganic origin. A circular marking may represent the remains of an indeterminate medusoid. Imprints on another block of sandstone resemble parts of the frond of *Charniodiscus*, but just as likely are disrupted pieces of a crinkled clay film. A possible trace fossil resembles *Gyrolithes polonicus* Fedonkin from the Tommotian of East Poland. Thus the finds in the Punkerri Hills do not provide a certain indication of the Ediacaran assemblage, but are not inconsistent with a late Precambrian to Early Cambrian age for the Punkerri Beds.

Glaessner (1969) reported a fragmentary impression of a frond-like fossil collected in a loose block on the Arumbera Sandstone, Amadeus Basin, east of Deep Well Homestead, S.S.F. of Alice Springs, central Australia. Jenkins & Gehling (1978) identified the specimen as an indeterminate species of *Charniodiscus*. Further study of the locality confirmed its likely placement in the lower half of the Arumbera Sandstone (*sensu stricto* Daily 1974 = Arumbera Sandstone I of Daily 1972) but revealed no new material. The Arumbera Sandstone may be broadly correlative with the Rawnsley Quartzite (Daily 1972).

The medusae described by Wade (1969) from the Central Mount Stuart Formation of the Georgina Basin, near Mt Skinner, are suggested to represent parts of an early scyphozoan radiation. One form, *Hallidaya brieri* Wade, has a rather wide distribution in the Georgina Basin where it is further documented by Kirschvink (1978) and Walter (1980) from Central Mount Stuart; Wade (1969) also indicated its occurrence in the Amadeus Basin, from probably near the top of the Arumbera Sandstone at Laura Creek just south of Valley Dam, W.S.W. of Alice Springs. These remains are seemingly younger in age than the Ediacara assemblage *sensu stricto* (Daily 1972; Glaessner 1977). The form identified by Glaessner (*In* Føyn & Glaessner 1979) as *Kullingia* aff. *concentrica*, and also from near Laura Creek, is apparently Early Cambrian. The Mt Skinner assemblage has not

¹Gauld, T. D. (1976) Trace fossils and the base of the Cambrian at Angapeena, northern Flinders Ranges, South Australia. B.Sc.(Hons) Thesis, University of Adelaide (unpublished).

been located in the Flinders Ranges and it is an open question as to whether the upper parts of the Arumberu Sandstone overlap the age of the Rawnsley Quartzite or are slightly younger.

Fine current rills (Dzuliński & Walton 1965), identified as the pseudofossil *Arumberia* Glaessner & Walter, occur widely in the sub-Cambrian to Early Cambrian sandstones of central Australia and are known at two levels in the late Precambrian of the Flinders Ranges. These inorganic marks are not considered to have any stratigraphic significance.

The preceding information provides a basis for consideration of potential stratotypes for an Ediacarian System.

Stratotypes

Harland (1974) made a detailed review of the extensively discussed problem of defining an internationally recognised boundary between the Precambrian and Cambrian, and also outlined major lines of evidence and criteria which might serve to identify divisions within the Proterozoic. With respect to possible stratotypes he stated: "Chosen successions will therefore be those transversing the boundary that are most complete and have the richest characters, or that are correlated directly with other rocks which have critical characters, and are well described and easy to of access". Comparable ideas are embraced in the guide to stratigraphic procedure of Holland *et al.* (1978). The geology of the Flinders Ranges satisfies some of Harland's requirements and provides thick, characteristic successions, though not without significant breaks. In the studies of Harland & Herod (1975) and Glaessner (1977, 1979b) the Ediacaran is linked by implication with the post-glacial, uppermost part of the Adelaidean of the Flinders Ranges. This part of the succession comprises the Wilpena Group of Dalgarno & Johnson (1964). The usage of Ediacaran and not "Ediacarian" (Cloud 1972, 1973, 1976a, b) is formalized, as the stem geographic names of other periods are unbroken and the endings of Period-names are not uniform (i.e. Jurassic and not Juristic). The locality name "Ediacara" is Aboriginal in origin and is reported by Goyder (1860) as "Idyakra".

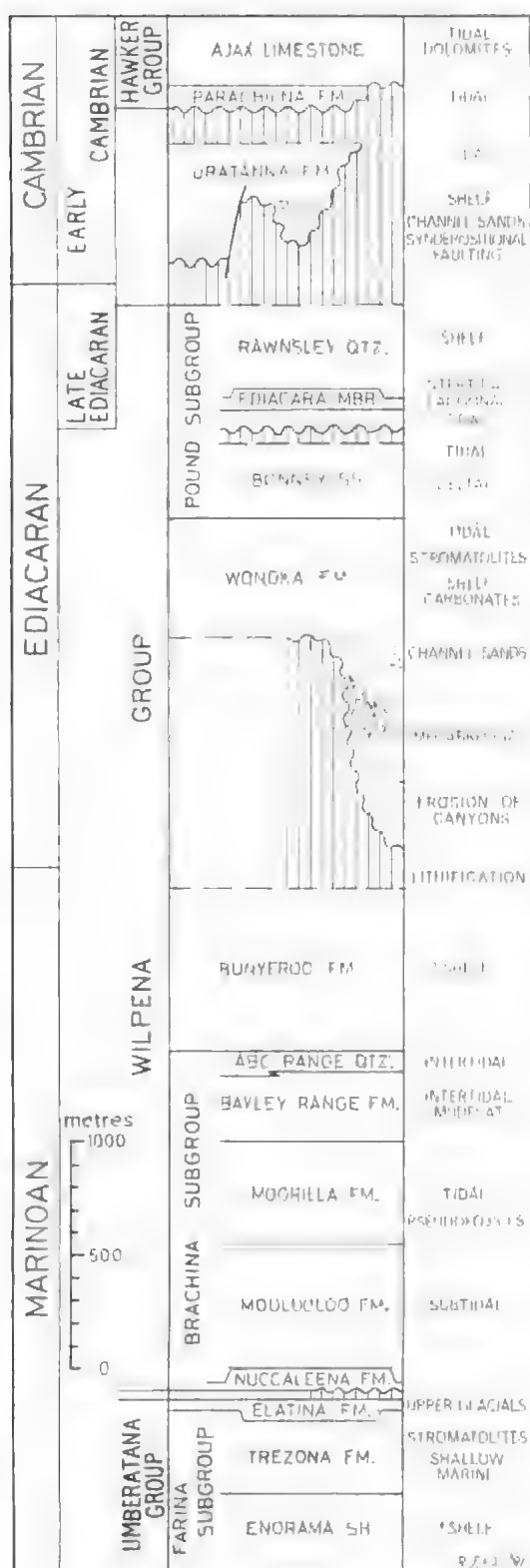
The Wilpena Group is placed in stratigraphic and regional perspective by Thomson (1969), Thomson *et al.* (1976) and Rutland

et al. (1981). Its potential correlatives in central Australia and northwestern Australia are indicated in figure 4 of Coats & Preiss (1980). The stratigraphic subdivision of the Wilpena Group in the central-western Flinders Ranges is shown in figure 2 of Jenkins *et al.* (1981) and a modified version of this is given here (Figure 2).

A boundary between the Precambrian and Cambrian is established by Daily (1972, 1973, 1976). In the northern Flinders Ranges this boundary is the surface of unconformity at the top of the Pound Subgroup (previously Pound Quartzite, Forbes 1971) and marking the base of the Uratanna Formation. The Uratanna Formation represents a single cycle of Early Cambrian deposition and locally attains a thickness of a little over 0.5 km. The Uratanna Formation is overlain unconformably by the Parachilna Formation, and in the central Flinders Ranges the Parachilna Formation rests directly on a surface of erosion developed on the Pound Subgroup. This erosion surface on the Pound Subgroup provides an upper boundary for the Ediacaran stratotype.

The characteristic Ediacaran assemblage of the Pound Subgroup is principally developed in a comparatively thin widespread interval of intercalated siltstones, fine sandstones, flaggy quartzites and medium to massive bedded quartzites in proximity to the base of the Rawnsley Quartzite (Wade 1970, Jenkins 1975b). This fossiliferous interval is termed the Ediacara Member of the Rawnsley Quartzite and its lithofacies development and environmental interpretations are discussed by Goldring & Curnow (1967) and Jenkins (1975b). The stratotype of the Ediacara Member is nominated as being Unit B of Goldring & Curnow (1967, fig. 5) in Ediacara Range at Greenwood Cliff, where it reaches a thickness of 30 m. The fossil assemblage of the Ediacara Member is the type example of the main Ediacaran biota. Rare impressions which may represent medusoids occur in the upper part of the Rawnsley Quartzite.

In the western and southern Flinders Ranges the base of the Rawnsley Quartzite, characterised by slightly feldspathic, clean white ortho-quartzites with frequent clay gall conglomerates, is sharply erosive on pinkish feldspathic sandstones included by Forbes (1971) in his division now recognised as the Bonney



Sandstone. In Parachilna Gorge, 1 km south of the type section of the Pound Subgroup, the surface of erosion below the Rawnsley Quartzite is irregular in form, with undercuts, and has a demonstrable relief of at least 10 m. Small, angular, ripped up blocks of the underlying sandstone are included in the orthoquartzites above the erosion surface and locally, chipped fragments of the underlying formation from minor gravel lenses in small downcuts of the erosion surface. This evidence suggests that the Bonney Sandstone had undergone partial lithification prior to the deposition of the Rawnsley Quartzite and indicates a temporal break. The Rawnsley Quartzite represents a transgressive cycle of marine deposition with the major fossiliferous parts of the Ediacara Member being tidal, back-barrier or lagoonal deposits (Jenkins 1975b).

Lower in the Wilpena Group the only certain indications of metazoan life are small, circular imprints of "medusoids" and simple trails (Form B of Glaessner 1969) located by Dr Mary Wade in the Bonney Sandstone (Jenkins *et al.* 1981). These remains indicate that the Bonney Sandstone properly belongs within the Ediacaran.

A major deficiency of the Wilpena Group as an Ediacaran stratotype is that as yet there is no indication of the radiation of the *Rangae*-like organisms and early members of the Petalonomae. However higher parts of the Wilpena Group have not been fully explored for metazoan remains. With reference to the Soviet section at Zimniygorsk it seems unlikely that the *Rangae*-like organisms should be found widely separated stratigraphically below the main Ediacara assemblage.

The base of the Wilpena Group is marked by a thin, distinctive widespread dolomite which forms a useful marker bed, the Nucaaleena Formation. This Formation is mostly conformable, though locally disconformable, above the partly glaciogenic Elatina Formation.

Fig. 2. Chart summarizing regional stratigraphy of younger part of Adelaidean succession and Early Cambrian in central and lower northern Flinders Ranges. Only upper part of Umberatana Group and lower part of Cambrian shown. Significant geological events, some environmental indicators, and environmental interpretations are summarized adjacent to stratigraphic column. Parts of section representing Ediacaran System are shown.

Shale datings for parts of the Adelaidean occurring in proximity to (and above) possible correlative glaciogenic deposits in the Kimberley Region, northwestern Australia, provide ages of 670 ± 84 Ma and 672 ± 70 Ma (Coats & Preiss 1980). The same authors review a dating of 676 ± 204 Ma for an apparent correlative of the "Brachina Formation" on the Stuart Shelf, west of the Flinders Ranges. Also in the Kimberley Region, a shale dating for a possible correlative of the Bunyerroo Formation gives the number 639 ± 47 Ma (Coats & Preiss 1980). Glaessner (1969) described the trace-like marking *Bunyerroo dalgarni* from the "Brachina Formation" but the biogenicity of this structure is now questioned (Jenkins *et al.* 1981). An intensive search has been carried out in the Brachina Subgroup (Plummer 1978a) for megascopic biotic remains, but structures so far located are also considered to be of inorganic origin (Plummer 1980; Jenkins *et al.* 1981). The limited available evidence as to the possible age of the Brachina Subgroup suggests it to be older than the estimated age of about 620 Ma for known early metazoans from elsewhere in the world. The Brachina Subgroup contains abundant sedimentary structures suggestive of mostly shallow-water deposition and the upper sheet sandstone (ABC Range Quartzite) is considered to reflect regressive conditions (Plummer 1978a). It and the overlying shales and siltstones of the Bunyerroo Formation are frequently reddish in colour, probably reflecting oxidative environments which are unlikely to be conducive for the preservation of either a microflora or higher algal remains, such as are well known at about this level in the Vendian (Sokolov 1977). Some greenish or unoxidized intervals are present (e.g. the Bayley Range Formation). In the southern Flinders Ranges and towards the east, the Brachina Subgroup changes to a thick green siltstone sequence, the Ulupa Siltstone, which is presumably unoxidized (Thomson 1969).

A potential placement of the lower boundary of the Ediacaran is at the base of the Nuccaleena Formation, which marks the termination of the Elatina glaciation (Plummer 1978b). The writer has no intention of debating the question as to whether Precambrian glaciogenic events are likely to be either synchronous or diachronous over wide land areas and differing parts of the globe. Such arguments have a circular component as there

is unlikely to be knowledge of the triggering mechanism of ancient glaciations. While the lithostratigraphic boundaries of glaciogenic intervals may be at once obvious and of great value for local and even regional studies (i.e. Coats & Preiss 1980), synchronicity of glacial events on a world wide basis has not been established. Kröner (1977) marshalled evidence favouring non-synchronicity for the late Precambrian glaciations of Africa, and suggested moving centres of glacial activity. The Schwarzwand glaciations of the Nama Group, unique in being correlative with sections bracketed by Precambrian metazoan fossils (*Rangia* and *Pteridium* below; trace fossils, *Cyclomedusa* Sprigg sp. and the lost single specimen of *Paramedusium africanum* Gürich above; Germs 1972a *et seq.*) seem to be significantly younger than the local Elatina glaciation (Jenkins *et al.* 1981). Placement of the stratotype boundary at the base of the Wilpena Group negates the underlying biostratigraphic implications of the Ediacaran, as there are no known unequivocal metazoan remains in close proximity. The time-significance of the Elatina glaciation is properly bound in the concept of the Marinoan 'Series' of Mawson & Sprigg (1950). Finally an association of the Ediacaran boundary with a glaciogenic event conceptually equates the interval with the Soviet Vendian, which has established priority. (The Marinoan has priority over both the Varangian and Vendian).

A second possible placement for the base of the stratotype is at the boundary of the Bunyerroo Formation and the Wonoka Formation; the latter contains glauconite and stromatolites and is of presumed marine origin (Thomson *et al.* 1976). One of the stromatolites is considered to be of Vendian affinity (Preiss 1977). With reference to the c. 640 Ma age for a likely correlative of the Bunyerroo Formation in the Kimberley Region, it seems possible that the time of deposition of the Wonoka Formation and succeeding Bonney sandstone may overlap or approximate the first appearance of megascopic metazoans elsewhere in the world; so far only a token effort has been made to locate metazoan fossils within the Wonoka Formation.

Over wide areas the Bunyerroo Formation passes gradually up into the Wonoka Formation. However, in the northern Flinders Ranges abnormally thick intervals of Wonoka sediments occur in several discordant troughs

which involve erosion of siltstones of the upper Bunyerroo Formation and sometimes as much as 1,070 m of pre-Wonoka deposits (Coats 1964). These troughs, described by Thomson (1969) as "submarine canyons", have a width of several km and show marginal breccia zones attributed to slumping. Comparable geological features have been studied by the writer in the vicinity of Pichi Richi Pass, near Quorn. Here the base of the Wonoka Formation is associated with a downcut surface and locally the Bunyerroo Formation is missing. The downcutting surface may evidence steep slopes and at one point truncates a major part of the ABC Range Quartzite. A megabreccia developed in the adjacent Wonoka Formation contains boulders with Bunyerroo Formation and ABC Range Quartzite lithologies. Individual boulders reach 3 m in maximum diameter and their size suggests lithification prior to their erosion. Boulders with a silty lithology show a repetitive fracturing at a steep angle to their internal bedding and suggestive of an incipient fracture cleavage. This fracturing appears to be at different orientations in adjacent blocks and not related to the fracturing of the matrix material (siltstone). There may be some local discordance between the folding of the ABC Range Quartzite and the Wonoka Formation but its significance is enigmatic. The geological features described suggest lithification of the ABC Range Quartzite and Bunyerroo Formation sediments prior to the time of Wonoka Formation deposition, and possible deformation before the strong erosive downcutting process took place. Professor C. C. von der Borch is studying comparable geological features elsewhere in the Flinders Ranges. These characteristics suggest that the 'normal' contact between the Bunyerroo Formation and the Wonoka Formation may represent a paraconformity (cf. Coats 1964).

The Wonoka Formation consists of green-grey calcareous siltstone, minor greenish or purple shales, intercalated thin-bedded to massive-bedded grey limestone, and some sandstone. Pelletoids forming a component of the limestones are considered as possibly being of faecal origin (von der Borch, *pers. comm.*). In the upper parts of the Wonoka Formation frequent intraformational conglomerates and oolitic limestones attest a shallow-water origin. Spectacular sole markings formed by currents are a persistent feature.

Sandy interbeds near the top of the Wonoka evidence tidal deposition and there are interbedded dolomitic shales, dolomites and sandstones at the passage into the intercalated pink, feldspathic sandstones and red-coloured, micaceous siltstones of the Bonney Sandstone. There is no evidence of any break in deposition between these two formations. Well rounded gravel lags associated with thin intercalated silts and sands in the lower parts of the Bonney Sandstone in some areas suggest a fluvial or deltaic influence. Sandstones with large-scale crossbedding may reflect channel development. Mud-cracked horizons, possible rain-drop markings and other sedimentary structures indicate frequent emergence and suggest a tidal environment for major parts of the Bonney Sandstone (Forbes 1971).

The potential placement of the lower boundary of the Ediacaran at the base of the Wonoka Formation is advantageous for the following reasons:

1. This boundary reflects a renewed phase of sedimentation following possible localised tectonism and associated erosive downcutting.
2. The Wonoka Formation is almost certainly marine and is known to include biogenic remains in the form of stromatolites. Its frequent greenish colour indicates that it is unoxidized and the variety of terrigenous and calcareous lithotypes offer maximum potential for the finding of a significant microflora or megascopic algal remains.
3. Fluctuating changes in sea level and subsequent transgression associated with the channelling at the base of the Wonoka may be reflected in other regions. Discovery of a significant microflora may provide a biological marker for these events.
4. The boundary between the Wonoka Formation and the Bonney Sandstone is transitional, suggesting continuous deposition. The Bonney Sandstone includes fragmentary evidence of metazoans.
5. Several fragmentary lines of evidence suggest that the time of deposition of the Wonoka Formation may be more or less equivalent to the first recorded appearance of well preserved metazoan remains elsewhere in the world. The Wonoka has not yet been intensively explored for megascopic fossils.

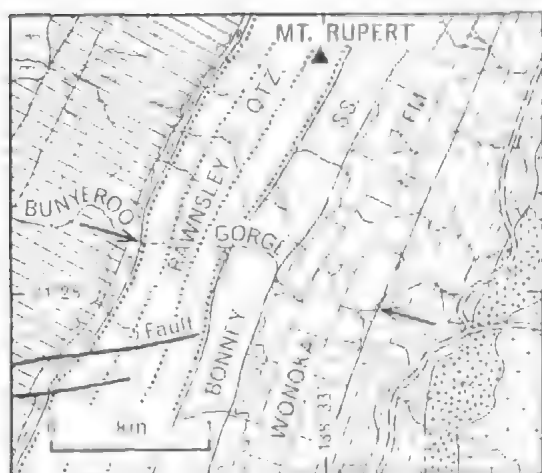


Fig. 3. Locality map showing Ediacaran stratotype, between arrows, and access tracks.

6. Placing the Ediacaran boundary at the beginning of a formation which is contiguous with the Pound Subgroup preserves the concept which equates this Period with the occurrence of early fossil metazoans.

Accordingly the stratotype for an Ediacaran System is formally nominated as comprising the whole of the Wonoka Formation and the Pound Subgroup. The type section is nominated as being at Bunyeroo Gorge (Figures 1 & 3), where the above stratigraphic intervals are excellently exposed and have a combined thickness of about 1320 m. Bunyeroo Gorge is also the type section of the Bonney Sandstone and Rawnsley Quartzite (respectively 305 m and 508 m thick, Forbes 1971), and contains a fossiliferous exposure of the Ediacaran Member (52 m thick) of the Rawnsley Quartzite. In the northern Flinders Ranges the Wonoka Formation and Pound Subgroup reach a cumulative thickness of about 4700 m.

The Rawnsley Quartzite in Bunyeroo Gorge is nominated as the stratotype for a Late Ediacaran Series characterised by a diverse suite of metazoan fossil remains probably reflecting an initial radiation of major surviving animal phyla. The index assemblage for the early part of this epoch comprises *Cyclomedusa davidi* sensu stricto, *C. plana* Glaessner & Wade, "*Medilganis*" *annulata* Sprigg, *Medusinites asteroides*, *Pinegia stellaris* Ediacaria flindersi, *Glaesmerina grandis*, *Dickinsonia costata*, *D. lissa*, *Tetradichidium heraldi*,

dicum, and *Pteridinium nenoxa*. The Ediacara Member of the Rawnsley Quartzite is established to be biostratigraphically equivalent to part of the Redkin substage of the Valdai Group in the Vendian of northern Russia (cf. Fedonkin 1981). Further correlation of different world Ediacaran sequences requires consideration of localized geological information outside the scope of the present study.

Conclusions

1. Over 20 years evolving ideas have developed concerning the geological time interval characterised by the soft-bodied metazoan assemblages of the terminal Precambrian. Continuing finds of such assemblages emphasize their potential value for biostratigraphy and of recent years there have been several informal designations of an Ediacaran Period.
2. Continuing geochronological studies associated with different known Ediacaran sites establish that early metazoan assemblages first appear at c. 640–620 Ma and that soft-bodied metazoans became diverse and frequent during the interval c. 600–570 Ma. The total time interval involved is comparable with that of the Cambrian, the base of which may be placed at c. 560 Ma or possibly even younger.
3. Evidence from central England establishes that the Ediacaran does not overlap the Cambrian, and that separate, sequential depositional events represent these time divisions. Ediacaran deposition in the English Charnian is terminated by folding, metamorphism, intrusion and erosion prior to a transgression beginning the Early Cambrian. The metamorphism and intrusive events are dated at c. 540–530 Ma.
4. The rocks containing the Ediacaran fossils are Precambrian in aspect, without the significant skeletal-bioclastic component typifying the Palaeozoic and the Phanerozoic as a whole.
5. The studies of Harland & Herod (1975) and Glaessner (1977, 1979b) link the Ediacaran with the post-glacial part of the Proterozoic Adelaidean succession, and by implication indicate a type area within the Flinders Ranges. The appropriate stratigraphic interval is the Wilpena Group.
6. Glaciogenic deposits (Elatina Formation) immediately preceding the Wilpena Group are argued to be of uncertain significance

for international correlation. Instead the base of the Ediacaran is placed at the lower boundary of the Wonoka Formation, the time of deposition of which is suggested to approximate that of the first known appearance of well preserved metazoans. The Wonoka Formation reflects marine transgression and possible later discoveries of a microflora, megascopic algae or even of Metazoa may offer a means of correlation.

7. The Ediacaran stratotype comprises the Wonoka Formation, Bonney Sandstone and Rawnsley Quartzite in Bunyeroo Gorge. The Wonoka Formation represents a shallowing upward cycle after an initial transgression; the Bonney Sandstone is generally paralic or regressive and is separated from the Rawnsley Quartzite by a widespread disconformity. The Rawnsley Quartzite represents a renewed cycle of transgression. The diverse metazoan assemblage in the Ediacara Member, near the base of the Rawnsley Quartzite, is considered to reflect the major evolutionary radiation of surviving invertebrate phyla. The exposure of the

Rawnsley Quartzite in Bunyeroo Gorge is nominated as the stratotype of a Late Ediacaran Epoch. An unconformity of regional extent separates the Ediacaran sequences in the Flinders Ranges from the succeeding Early Cambrian.

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AZOLLA CAPRICORNICA SP. NOV. FIRST TERTIARY RECORD OF AZOLLA LAMARCK (SALVINIACEAE) IN AUSTRALIA

BY C. B. FOSTER & W. K. HARRIS

Summary

Megaspores and massulae of *Azolla capricornica* sp. nov. are the first recorded Tertiary examples of the water fern *Azolla* Lamarck 1783 from Australia and are the oldest known representatives of the genus in the Southern Hemisphere. Extensive TEM and SEM studies show that the megaspore apparatuses have randomly distributed vacuolae, rather than defined float structures. It is this feature which readily distinguishes this species from the widespread extant species, *Azolla filiculoides* Lamarck. Columellae (sensu Fowler & Stennett-Willson 1978) are not discernible. The microspore massulae possess glochidia with anchor-shaped tips, and each contains as many as 12 laevigate to finely granular microspores.

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SUMMARY

FOSTER, C. B. & HARRIS, W. K. (1981) *Azolla capricornica* sp. nov. First Tertiary record of *Azolla* Lamarck (Salvinaceae) in Australia, *Trans. R. Soc. S. Aust.* **105** (4), 195-204, 11 December, 1981.

Megaspores and massulae of *Azolla capricornica* sp. nov. are the first recorded Tertiary examples of the water fern *Azolla* Lamarck 1783 from Australia and are the oldest known representatives of the genus in the Southern Hemisphere. Extensive TEM and SEM studies show that the megaspore apparatuses have randomly distributed vacuolae, rather than defined float structures. It is this feature which readily distinguishes this species from the widespread extant species, *Azolla filiculoides* Lamarck. Columellae (*sensu* Fowler & Stennett-Willson 1978) are not discernible. The microspore massulae possess glochidia with anchor-shaped tips, and each contains as many as 12 laevigate to finely granular microspores.

The fossils are of Middle to Late Eocene age, and were recovered from The Narrows Beds, Narrows Graben, Queensland. Their presence suggests a relatively still fresh water environment of deposition. Known occurrences of *Azolla capricornica* sp. nov. are confined to presently tropical areas of Queensland. Its phylogenetic relationship to the Quaternary and extant species, *A. filiculoides*, found in temperate and sub-tropical regions of Australia, remains obscure.

Introduction

The first Australian fossil occurrence of members of the free-floating heterosporous fern *Azolla* Lamarck 1783 was reported by Duigan & Cookson (1957) from Quaternary sediments in Victoria. They identified their specimens with an extant species, *A. filiculoides* var. *rubra*, which is common and widely distributed in Australia. It grows on areas of relatively still freshwater. Although records of the genus are widespread in Late Cretaceous and Tertiary sediments of the northern hemisphere (see Collinson 1980), *Azolla* has not been reported previously from southern hemisphere sequences which are older than Quaternary.

The species described in this paper is readily distinguished from *A. filiculoides*, and congeners. However, we assume that the ecological requirements of *A. capricornica* were similar to that of extant *Azolla*, although its geographic range seems to be confined to the presently tropical areas of Australia. Despite apparently suitable biofacies in the Tertiary coastal and intracratonic basins of southern parts of the continent, no examples of *Azolla* have been found in the many areas studied.

Geological Setting

The Narrows Beds, defined by Kirkegaard, *et al.* (1970), occur in a northwest-southeast trending, graben-like structure which is bounded by Curtis Island and the Rundle-Mt Laramie Ranges (Fig. 1). The Beds include a thick sequence (500+ m) of oil shales, known as the Rundle Oil Shale deposit, currently being assessed for commercial hydrocarbon exploration. Lindner & Dixon (1976) have given a detailed description of the Rundle deposit, which includes at least six oil shale units or seams (of the Rundle Formation) which are intercalated with green-grey montmorillonitic claystones, mudstones, carbona-

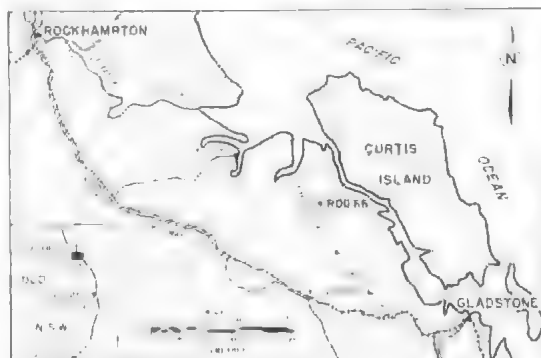


Fig. 1. Position of drill-hole RDD66, in the Narrows Graben.

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† Western Mining Corporation Ltd, 168 Greenhill Rd. Parkside, S. Aust. 5063.

THE NARROWS BEDS	CURLEW FORMATION	
	BUREHOLE FORMATION	Kerosene Creek seam Telegraph Creek unit Mandurah Creek seam Humpy Creek seam Brick Kiln seam Ramsay Crossing seam
	WORTHINGTON FORMATION	

Fig. 2. Stratigraphy of the Narrows Beds, Narrows Graben, Queensland. Units are presented in descending stratigraphic order.

aceous shales, minor impure carbonates and lignites. Figure 2 depicts the local stratigraphy.

The lithostratigraphic names have been reserved with the Australian Central Register of Stratigraphic Names and will be formalised in a paper by Henstridge & Missen (1981).

Although the stratigraphic boundaries of The Narrows Beds have not been established with certainty, the occurrence of freshwater ostracods, often in enormous numbers in mudstones and oil shales, suggests that the Beds were deposited in lakes that were 'largely shallow but probably of a permanent nature' (Beasley 1945). As discussed below, the presence of *Azolla* within the Curlew Formation and Kerosene Creek seam (in RDD 66, 139.45 m) further supports a wholly non-marine environment of deposition.

Foster (1979) suggested that a palynological assemblage from a core of the Curlew Formation (designated at that time as the Watte Creek seam) intersected in borehole RDD 66 at 37.40 m was of Late Eocene to Late Oligocene age. This range can be narrowed to Middle to Late Eocene using comparative ranges of taxa from southern Australia (W. K. Harris, unpublished data).

Material and Methods

Azolla glochidia were first recognised in strew slides prepared by standard procedures for routine palynological examination at the Geological Survey of Queensland. Further specimens of massulae and megaspores were isolated by washing the disaggregated sediment after digestion in 70% hydrofluoric acid through a 200 mesh/inch sieve. Individual

megaspores and massulae were picked from the coarse fraction and either mounted for SEM study or bleached in 1% sodium hypochlorite solution and mounted in glycerine jelly on microscope slides for examination by transmitted light. Those selected for SEM study were gold coated and examined with a Cambridge S600 SEM at the University of Queensland or with an ISI Super Mini SEM at the Geological Survey of South Australia.

Ubleached specimens were selected for study by both conventional transmitted light and transmission electron microscopy (TEM). TEM sections were prepared and studied at the Electron Microscope Unit, University of Queensland.

Specimens are retained in the palynological collection at the Geological Survey of Queensland; catalogue numbers prefixed Q are those of that institution. All photomicrographs are from unretouched negatives and prints. Magnifications are given for each figure. Coordinates of specimens, given after slide numbers are from a Zeiss Photomicroscope III No. 1369 housed at the Geological Survey of Queensland. SEM negatives prefixed MIS are held in the above repository; all TEM negatives are stored at the Electron Microscope Unit, University of Queensland. All specimens are from the Type Material.

Systematic Description

FAMILY SALVINIACEAE Dumortier

Genus *AZOLLA* Lamarek 1783

Azolla capricornica Foster & Harris sp. nov.

FIGS 3-8

Diagnosis: Megaspore apparatus without float structures and lacking discernible columella (*sensu* Fowler & Stennett-Willson 1978). Proximal hemisphere of megaspore proper surmounted by dense, hairy, conical perinal structure, within which vacuolae are randomly developed and distributed (vacuolae best seen in TEM sections, barely discernible using conventional light microscopy). Cone commonly larger than remainder of megaspore apparatus; towards cone apex, outermost hairs are commonly fused to delimit a \pm smooth apical area (best seen using SEM). Basal perimeter of cone defined by a \pm well developed collar. Below collar, and covering distal hemisphere of megaspore, perine (differentiated into en-

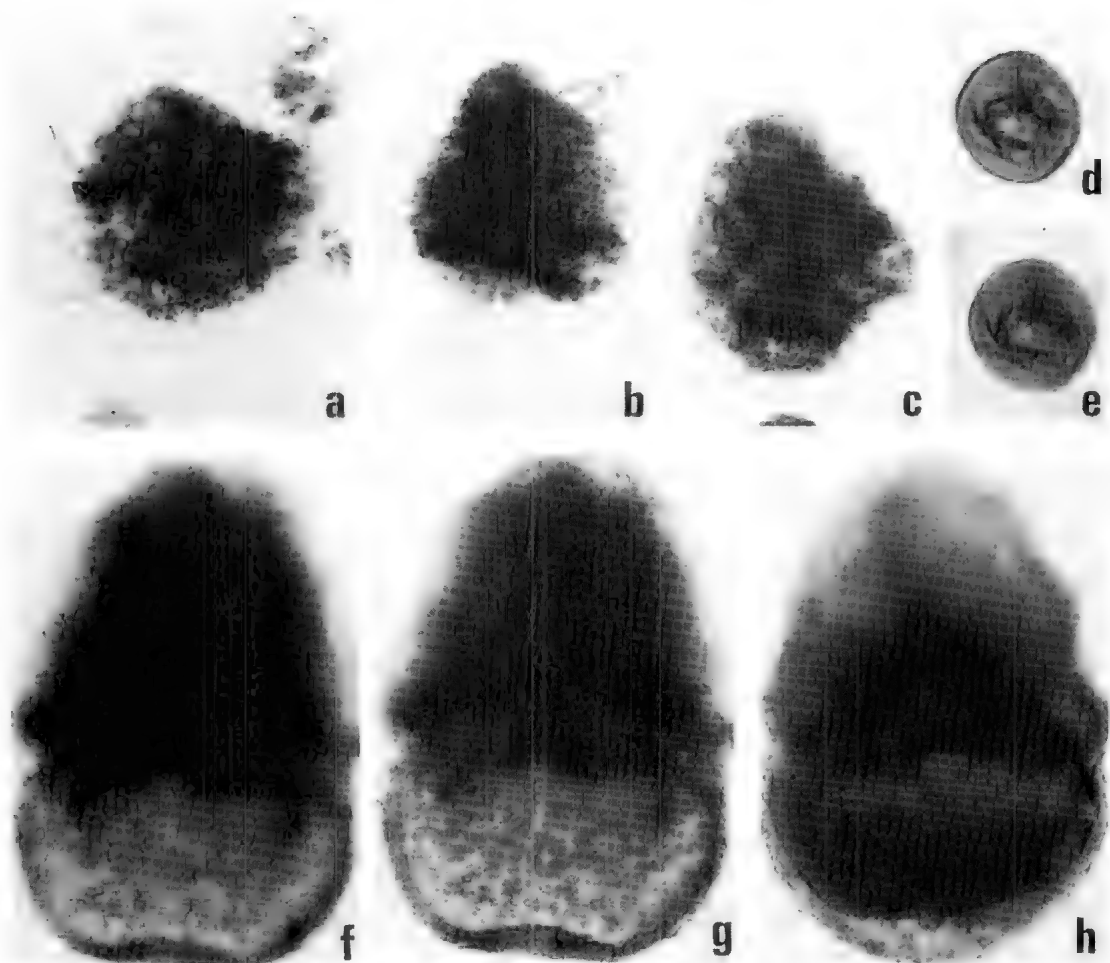


Fig. 3. *Azolla capricornica* Foster & Harris sp. nov. a-c. Microspore massulae. a. Holotype ($\times 170$); slide 9884, 9.5 98.0, Q130. b. Paratype ($\times 205$); slide 9884, 21.5 119.9, Q131. c. Paratype ($\times 209$), note microspores; slide 9884, 11.2 120.8, Q132. d, e. Microspore ($\times 500$), proximal and distal foci respectively; slide 9884, 3.2 96.6, Q133. f-h. Megaspore apparatuses. f, g. Holotype ($\times 139$) at differing foci; slide 9883/9, 11.7 108.2, Q134. h. Paratype ($\times 118$), showing folded megaspore exine; slide 9883/6, 10.5 107.5, Q135.

doperinal and exoperinal layers) less hairy and coarsely reticulate. Reticulum perfect to imperfect; lumina $7-30\ \mu\text{m}$ wide; muri of fused, intertwined, irregular regulae-like elements, $5-12\ \mu\text{m}$ in overall width, up to $20\ \mu\text{m}$ high. A central canal, extending from proximal megaspore to apex of cone may occur in some specimens. Microspore massulae irregular mostly spherical to ovoid, dispersed or attached to megaspores; often sterile or with as many as 12 microspores in each. Microspores, spherical, trilete; laesurae simple or with narrow, low labra, almost reaching to equator; exine $1.5-2\ \mu\text{m}$ thick, laevigate to

finely granular. Surface of massulae bearing $3-20+$ glochidia. Each glochidium has anchor-shaped tip, mostly with two recurved hooks (each $10-14\ \mu\text{m}$ in length from apex of tip), extremely rarely with single recurved hook at terminus. Glochidia mostly aseptate, very few with one or two septa; each $\text{ca } 0.5\ \mu\text{m}$ thick, strap-like; $3-15\ \mu\text{m}$ wide, constricted at point of origin and immediately below anchor-shaped tip, maximum width about midway along length ($42-93\ \mu\text{m}$). Exine of megaspore (in surface view) minutely punctate or granulate, with irregularly distributed cavities in section, $5-8\ \mu\text{m}$ thick; perine $13-28\ \mu\text{m}$ thick.

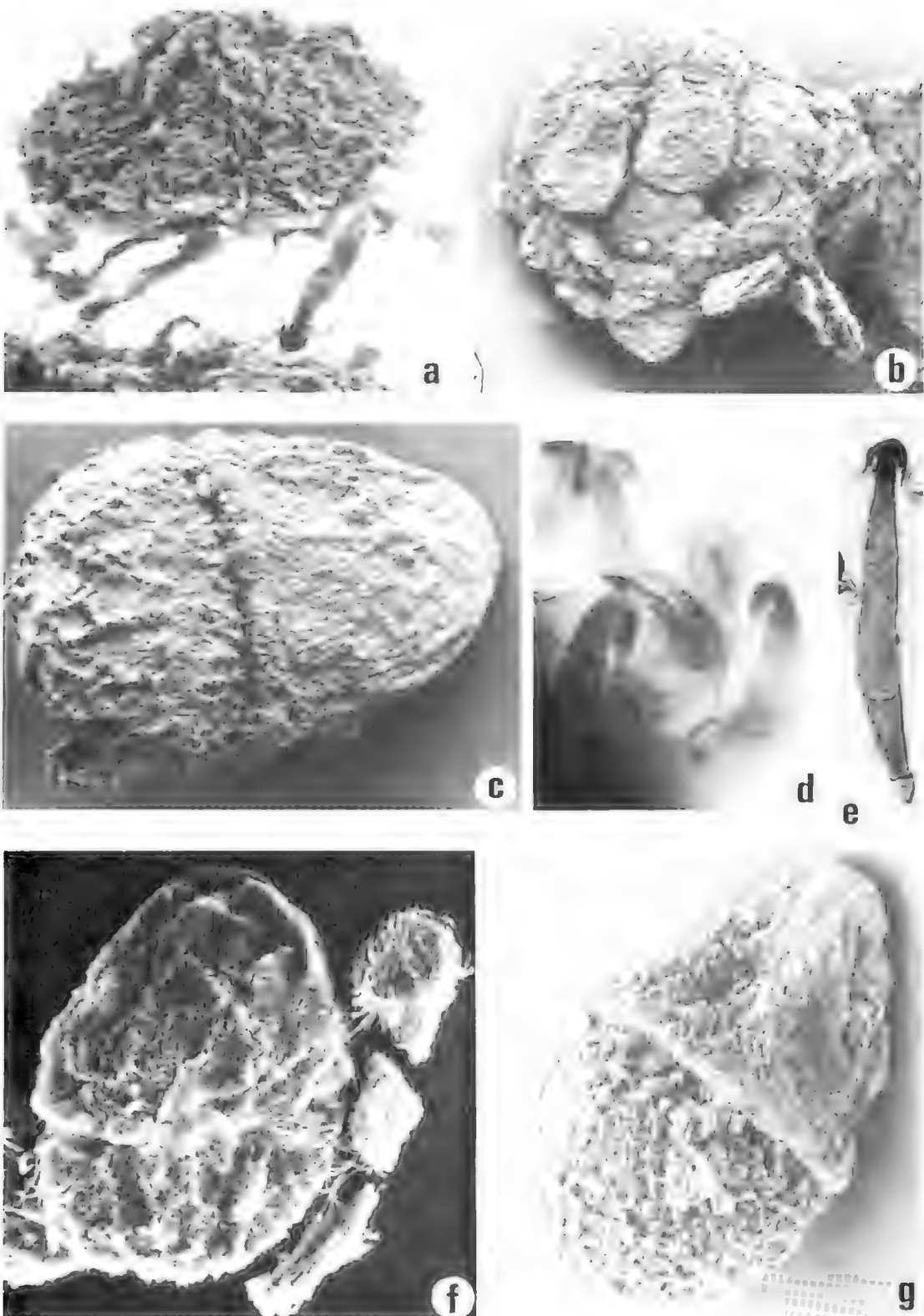


Fig. 4.

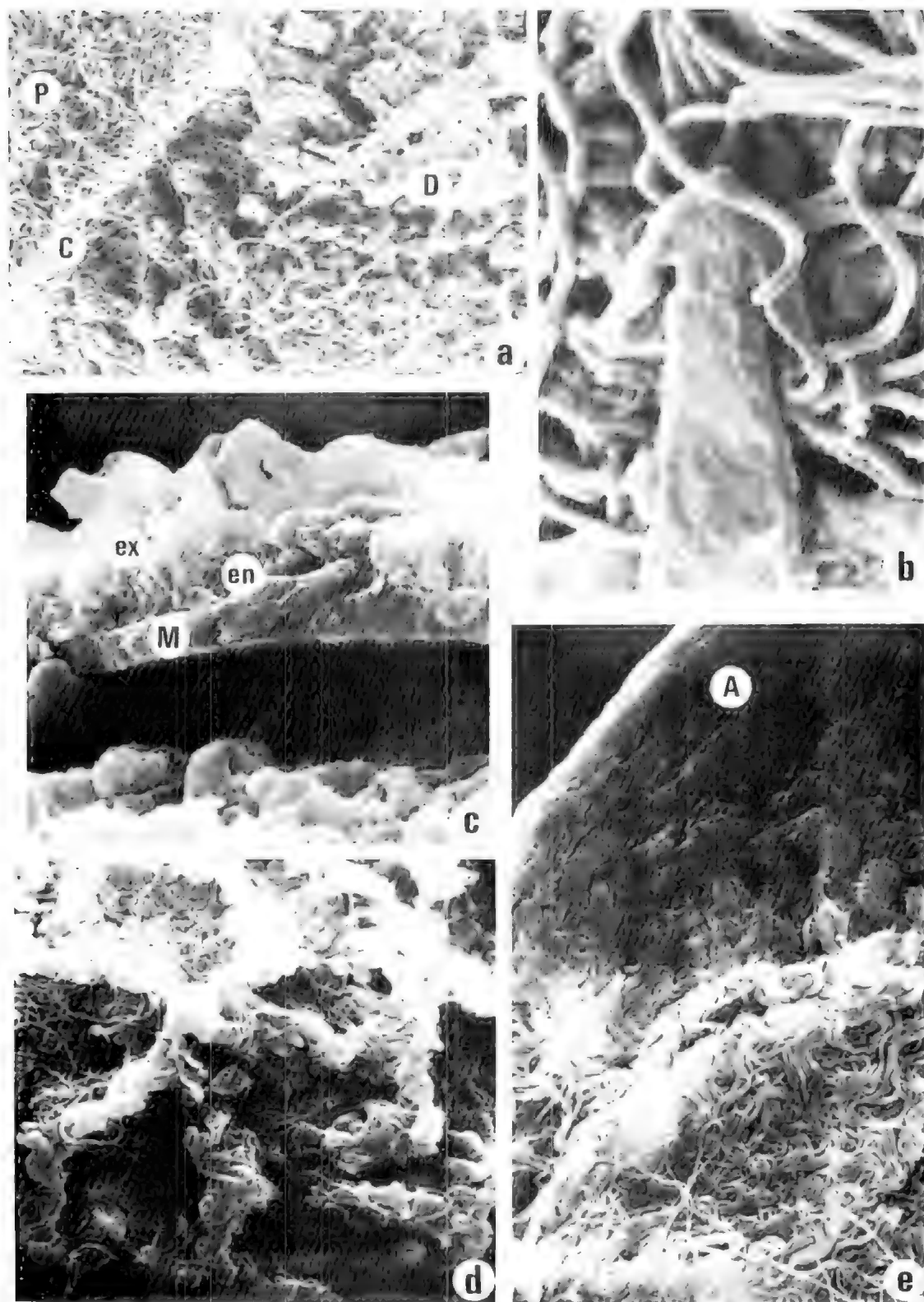


Fig. 5

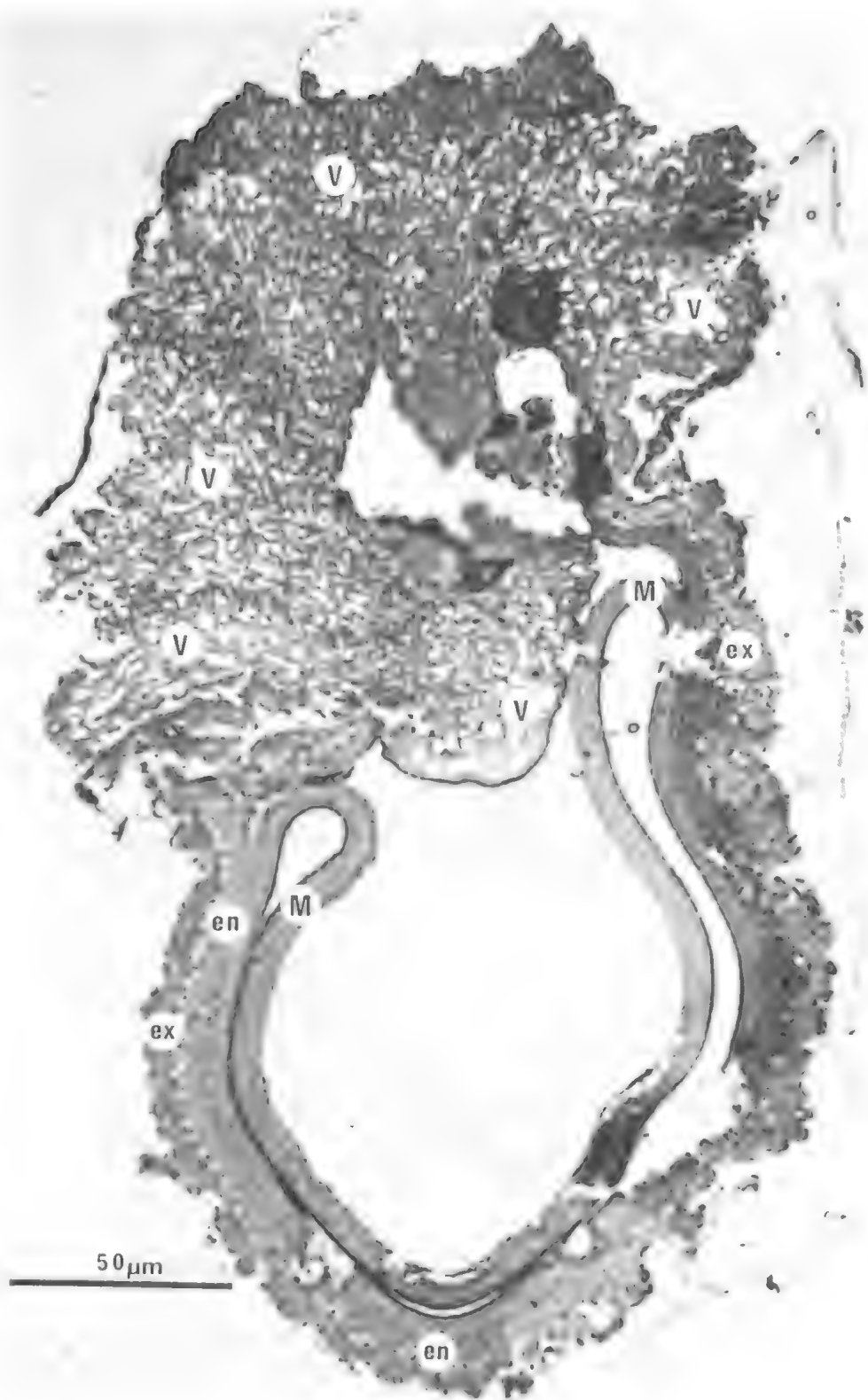


Fig. 6

Dimensions: Megaspore apparatus: total length 410–560 μm ; breadth (widest) 340–400 μm (50 specimens). Microspore massulae: 105–240 μm (maximum diameter 30 specimens); microspores 24–36 μm (equatorial diameter). **Holotype:** Megaspore apparatus, Fig. 3, f.g; single mount, slide 9883/9, coordinates 11.7 108.2, Q134. Total length 465 μm ; maximum width, at collar, 332 μm . Megaspore wall 5–10 μm thick, minutely granulate. Perine over distal hemisphere of megaspore 10.5–13.5 μm thick; imperfectly reticulate, lumina 7–30 μm wide, muri 3–12 μm wide.

Microspore massula, Figure 3a; strew mount, slide 9884, coordinates 9.5 98.0, Q130. Outline $\frac{1}{2}$ circular, 176 μm in diameter. Four microspores are visible, up to 32 μm in diameter, exine 1.75 μm thick. Eight glochidia are visible, maximum length discernible 63 μm ; width 3.5–8.5 μm .

Type locality: Diamond drill hole RDD 66 at 100.25 m. Grid reference 7382IN 29950E. GLADSTONE 1:100 000 sheet no. 9150; Rockhampton 1:250 000 Sheet Area, Queensland.

Type horizon: The Nattows Beds, Curlew Formation, Seam lithology: grey-brown carbonaceous mudstone. Age: Middle to Late Eocene.

Derivation of name: From the Tropic of Capricorn; present known occurrences of *A. capricornica* are confined to deposits which straddle the Tropic, between 22° and 24°S.

Comparison and remarks. A simplified terminology has been used to describe specimens

of *Azolla capricornica* sp. nov. and the accompanying illustrations (Figs. 3–8) clarify the morphology of the species. Floats, as currently recognised (see Martin 1976, Fowler & Stennett-Willson 1978, Collinson 1980) have not been recognised in the presently described species and it is their absence which separates *A. capricornica* from the various members of *Azolla* which have 3–24 floats (see Collinson 1980, for summary). *A. capricornica* is therefore readily distinguished from the Australian Quaternary and extant species of *A. filiculoides* which has a three float megaspore apparatus (see Fowler & Stennett-Willson 1978, for recent description).

Comparison with taxa which are considered to possess only a single float-like structure or columellate-float, namely, *Azolla simplex* Hall 1969; *A. primaeva* (Arnold) Penhallow 1955; and *A. genesiana* Hills & Weiner 1965 must be at a relatively superficial morphologic level because of the lack of comprehensive structural information about them. *A. simplex* is distinguished by its finer reticulum with lumina of 2–6 μm and muri ca 1 μm wide, and its loosely attached float-like structure; *A. primaeva* has a less conical, proximal perinal structure, and a non-reticulate distal perine, and massulae details differ (glochidia are much narrower); *A. genesiana* is distinguished by, amongst other details, its slender glochidia with irregularly shaped tips. Also, because of the lack of structural detail, *A. capricornica* has not been assigned to Section Simplicispora (Hall 1970) which was created to accommodate the above three species.

Fig. 4. a, SEM ($\times 675$), neg. no. MIS 29; microspore massula attached to megaspore apparatus; specimen not recovered. b, SEM ($\times 120$), neg. no. MIS 22; microsporangium, showing cluster of microspore massulae; specimen not recovered. c, SEM ($\times 172$), neg. no. MIS 13; megaspore apparatus; note smooth apical area (na), cone, specimen not recovered. d, Glochidium ($\times 1000$) with single recurved hook at terminus; slide 9884, 18.0 107.6, Q136. e, Isolated glochidium, (DIC, $\times 635$), showing constrictions at point of attachment to massula and immediately at base of tip; slide 9885, 14.2 91.9, Q137. f, SEM ($\times 150$) neg. no. 200/19; megaspore apparatus with 3 massulae attached; specimen not recovered. g, SEM ($\times 200$) neg. no. MIS 31; megaspore apparatus showing smooth apical area, coarsely reticulate perine, well defined collar; specimen not recovered.

Fig. 5. a, SEM ($\times 500$), neg. no. MIS 32; detail of collar area, (c) with reticulate distal perine (D) and hairy perine of proximal cone (P), specimen not recovered. b, SEM ($\times 5000$), neg. no. MIS 26; glochidium with anchor-shaped tip and two recurved hooks; note constriction at base of tip. Specimen attached to megaspore apparatus, not recovered. c, SEM ($\times 1500$), neg. no. 200/14; section of megaspore apparatus; (M) megaspore wall, (en) endoperine and (ex) exoperine; specimen not recovered. d, SEM ($\times 750$), neg. no. 200/17; reticulate distal distal perine, showing muri of fused, intertwined rugula-like elements, specimen not recovered. e, SEM ($\times 525$), neg. no. 200/28; megaspore apparatus showing smooth area delimited by fused hairs at apex (A), specimen not recovered.

Fig. 6. LS of megaspore apparatus, section ca 1 μm thick, bar scale 50 μm . Megaspore wall (M), collapsed and infolded; endoperine (en) and exoperine (ex) well defined. Randomly developed vacuolae in proximal cone indicated by (V); slide 9883/10, 12.9 77.2, Q138.



Fig. 7. TEM ($\times 1050$) neg. nos 7813, 7814, 7815. LS of megaspore apparatus. Megaspore wall (M) infolded as in Figure 6, note irregularly shaped, randomly distributed cavities in wall; (en) endoperine; (ex) exoperine; (V) detail of vacuolae developed in proximal perine.

Discussion

Collinson (1980) has reviewed the possible phylogenetic implications attributed to the various structural differences or morphotypes (which are manifest in float number, mode of attachment of floats; microspore massulae, shape of glochidia) within *Azolla*. She concurred with Hall (1969), and Martin (1976) that four lineages may be recognisable within the genus. Members of the lineages respectively possess 1, 3, 9 and 9+ floats. In this context it is worthwhile emphasising that *A. filiculoides* and *A. capricornica* are separable on the basis of 'float' number, 3 and 1(o?) respectively. The term 'float' is used here in the sense of Fowler (1975). Using this criterion it would be imprudent to suggest that *A. capricornica* was the ancestral form of the Australian Quaternary and extant species.

Azolla capricornica is presently known in oil shale deposits in the Narrows Graben and to the northwest in the Duaringa and Yaamba Basins (Foster unpublished). These deposits straddle the Tropic of Capricorn, between 22°

and 24° (for localities see Swarbrick 1974). Members of the genus have not been recorded from coeval sediments from more southern coastal Tertiary basins, or from intracratonic sediments of central Australia. On present evidence, it seems that *Azolla* entered Australia from more northern and tropical latitudes at least during the Middle to Late Eocene. Should the hypothesis of northern entry be correct, even earlier occurrences of *Azolla* may yet be found in the late Cretaceous of northern Australia.

Palaeoecology

We draw attention to the value of *Azolla* as an environmental indicator in present day environments. It is mostly a warm-temperate to tropical genus inhabiting freshwater. Ideal growing conditions for *Azolla* are still water where the effects of turbulence and periodic flooding will not fragment the colonies. Should intermittent turbulence occur, the fern has the ability to regenerate rapidly once favourable conditions are restored. The fine grained nature of the enclosing sediment at Rundle and the high sapropel content of the acid

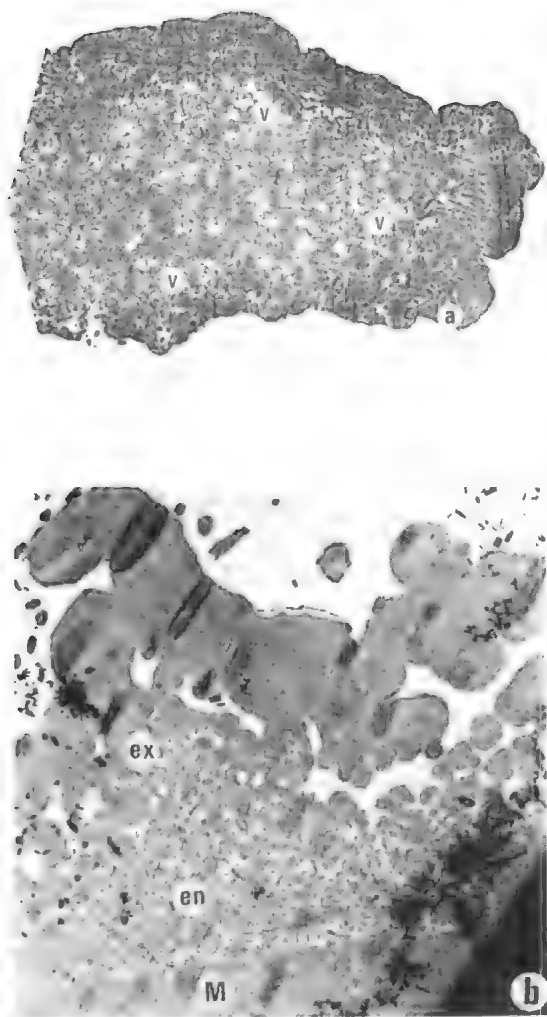


Fig. 8. a. TEM ($\times 1000$), neg. nos 7895, 7896. TS section taken about midway between collar and apex of cone. Large randomly developed vacuolae (V) of (?) endoperine surrounded by denser exoperine. b. TEM ($\times 3000$), neg. no. 7812. LS section of megaspore apparatus; (M) megaspore wall, (en) endoperine, (ex) exoperine.

insoluble residue together with the abundance of *Azolla* megaspores, indicates that sedimentation occurred in a freshwater environment with little turbulence and low detrital sediment influx.

Under such conditions any water flow would be slow, and it is likely that mats of *Azolla* colonised surface waters. Such mats would largely reduce available light in the water column, leading to anaerobic and reducing conditions; nevertheless blue-green algae and certain other plant life could survive under these conditions. Ashton & Walmsley (1976) for example, have drawn attention to the importance of the blue-green algal symbiont (*Anabaena azollae*) in the life cycle of *Azolla filiculoides* where it is responsible for nitrogen fixation, allowing the fern to colonise nitrogen-deficient environments.

The palaeo-ecological setting proposed is restricted to those sections of the Narrows Beds which contain *Azolla*. Nevertheless the overall environmental setting is supported by petrographic studies of Hutton, *et al.* (1980) who described the dominant maceral of the Rundle oil shales as a finely bounded lamella alginite (Alginite B) interbedded with matter in well-laminated sediments. They used the term "lamosite" for this maceral type and further, suggested that it was derived from algal mats. All the evidence is consistent with Beasley's (1945) suggestion that the beds were deposited in shallow and probably permanent lakes.

Acknowledgements

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A PARAPATRIC BOUNDARY BETWEEN TWO SPECIES OF REPTILE TICKS IN THE ALBANY AREA, WESTERN AUSTRALIA

BY C. M. BULL & D. R. KING

Summary

The distribution of populations of a tick morphologically similar to *Aponomma hydrosauri* was mapped near Albany in Western Australia. This taxon occupies an area of approximately 60 × 40 km. To the west its boundary appears to coincide with the edge of the jarrah forest belt. To the north and east its distribution abuts that of the more widespread reptile tick, *Amblyomma albolimbatum*. There is no obvious ecotone associated with this parapatric boundary. It is suggested that the boundary is maintained by an interaction between the two species. The stability of the boundary is not yet known, but one explanation of the present pattern of distribution is that *Amb. albolimbatum* is gradually expanding its range into areas previously occupied by *Ap. Hydrosauri*.

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Summary

BULL, C. M. & KING, D. R. (1981) A parapatric boundary between two species of reptile ticks in the Albany area, Western Australia, *Trans. R. Soc. S. Aust.* **105** (4), 205-208, 11 December, 1981.

The distribution of populations of a tick morphologically similar to *Aponomma hydrosauri* was mapped near Albany in Western Australia. This taxon occupies an area of approximately 60 × 40 km. To the west its boundary appears to coincide with the edge of the jarrah forest belt. To the north and east its distribution abuts that of the more widespread reptile tick, *Amblyomma albolimbatum*. There is no obvious ecotone associated with this parapatric boundary. It is suggested that the boundary is maintained by an interaction between the two species. The stability of the boundary is not yet known, but one explanation of the present pattern of distribution is that *Amb. albolimbatum* is gradually expanding its range into areas previously occupied by *Ap. hydrosauri*.

Introduction

Smyth (1973) first described parapatry in the tick species, *Aponomma hydrosauri*, *Amblyomma limbatum* and *Amb. albolimbatum* in South Australia. All three species infest the same reptile hosts. In any one place only one of the three species is found, and their distributions abut at common boundaries. Investigations have failed to provide a satisfactory explanation of the mechanisms which prevent range overlap at the boundaries (Bull & Smyth 1973, Sharrad¹, Bull, Sharrad & Peiney 1981). Smyth (1973) suggested two hypotheses. One hypothesis is that the boundaries follow environmental ecotones, and that at least one of the contacting species is poorly adapted for conditions across the boundary. This hypothesis was supported by the results of a detailed study near Mt Mary, South Australia, where the boundary between *Ap. hydrosauri* and *Amb. limbatum* coincides with the sharp vegetational change from mallee scrub to open woodland; however transplant experiments^{1,2} have failed to demonstrate reduced fitness of either species across the ecotone (Bull *et al.* 1981). At other boundaries between pairs of these species environmental changes are less obvious (Smyth 1973, Bull *et al.* 1981).

The second hypothesis proposes that parapatric boundaries are maintained by ecological

interactions between the tick species, resulting in the exclusion of one of them from the range of the other. The outcome of the interaction may be reversed where there is an environmental change, such as at an ecotone. Thus stable boundaries will form at ecotones, but boundaries will be established also wherever the ranges of two of the species contact, independently of the environmental conditions. A prediction is that where the ranges of two species meet in other areas parapatry would be expected also.

In southwestern Australia, *Amb. albolimbatum* is the common reptile tick but another species, morphologically similar to *Ap. hydrosauri*, was found by C.M.B. near Albany in southern Western Australia (Smyth 1973). The taxonomic status of this population is under investigation but here it will be referred to as "*Ap. hydrosauri*". Sharrad¹ and Sharrad & King (1981) confirmed its presence in at least four small isolated areas along the south coast of Western Australia. Their collections were sufficiently detailed to show that there was a parapatric boundary between *Amb. albolimbatum* and *Ap. hydrosauri* at Cape Naturaliste (Sharrad & King 1981), which may coincide with a vegetational ecotone (Bridgewater & Zimmitt 1979). We describe

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¹ Sharrad, R. D. (1980) Studies of the factors which determine the distributions of three species of South Australian ticks. Ph.D. Thesis, University of Adelaide, (unpublished).

² Peiney, T. N. (1981) The interaction of two parapatric tick species with their off host environment. Ph.D. Thesis, Flinders University, (unpublished).

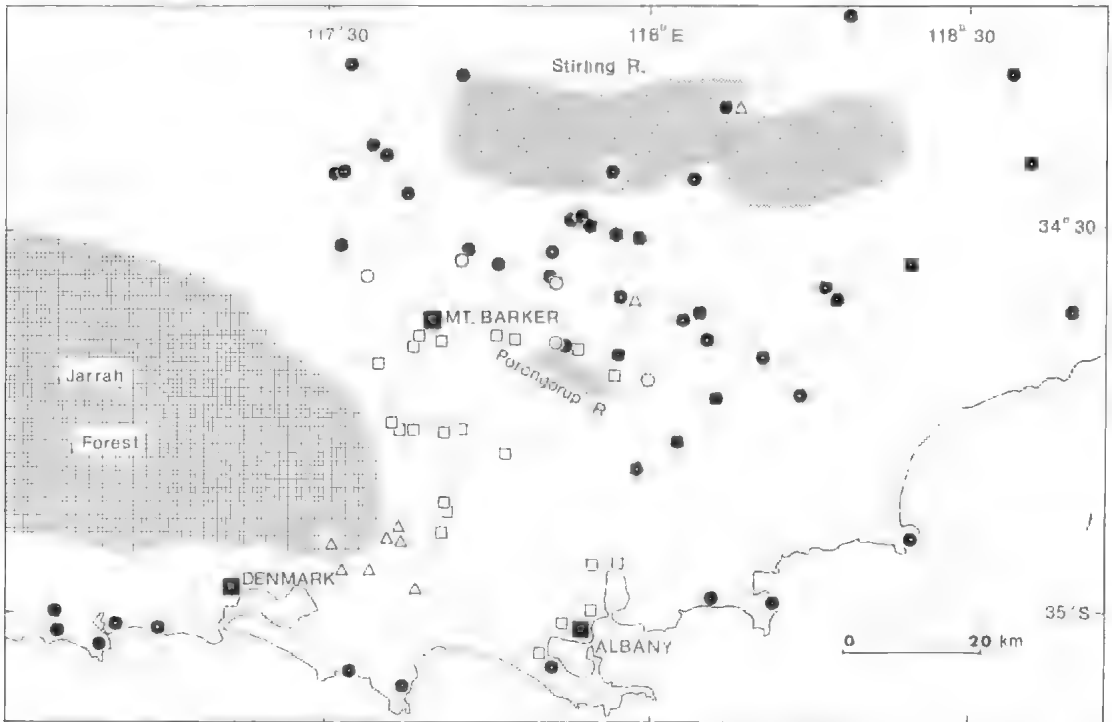


Fig. 1. Distribution of *Aponomma hydrosauri* (open squares) and *Amblyomma albolimbatum* (closed circles) in the study area. Lizards with both species attached are shown with open circles, and those with no ticks attached, by open triangles.

investigations of the prediction that there is parapatry between the species near Albany.

Materials and Methods

Earlier records from a general survey of reptile ticks in Western Australia (Sharrad & King 1981) were supplemented with additional data collected in 1979 and 1980, and a detailed survey made in October 1980 of the area around Albany (Figure 1). Lizards, mainly *Trachydosaurus rugosus*, were captured as they crossed the roads or basked on the roadsides, and were examined for attached ticks.

Only *Ap. hydrosauri* and *Amb. albolimbatum* were found on *T. rugosus*. Adult ticks but not larvae and nymphs could be easily identified in the field and the immature stages were removed for later identification. A simple distinguishing feature is that *Amblyomma* species have eyes but *Aponomma* species lack them (Roberts 1970).

Other data came from road-killed hosts. Individuals of *T. rugosus* are commonly run over by vehicles, and some ticks remain attached to their dead host for several days (unpubl. observ.).

Other reptile species were examined when encountered. One blue tongue skink (*Tiliqua occipitalis*) and six freshly-killed brown snakes (*Pseudonaja nuchalis*) were examined, but had no ticks attached. Two snakes (no identification provided) and six goannas (all *Varanus rosenbergi*) from the area previously had been found infested by the tick species *Aponomma fimbriatum*.

Results

The distributions in the study area of the tick species, *Amb. albolimbatum* and *Ap. hydrosauri*, attached to *T. rugosus* are shown in Figure 1. The range of *Ap. hydrosauri* is 60 km (north-south) \times 40 km (east-west). To the north and east its distribution abuts that

of *Amb. albolimbatus* which is widely distributed in southern Western Australia (Sharrad & King 1981). *Amb. albolimbatus* was not found within the distribution of *Ap. hydrosauri*, except in a narrow boundary zone (Figure 1), where both species were found together. Five host individuals collected in the boundary zone had both tick species attached to them. The width of the overlap zone is not known, but at the northern boundary there were less than 10 km separating hosts with only *Ap. hydrosauri* from hosts with only *Amb. albolimbatus*.

To the west, the distribution of *Ap. hydrosauri* abuts with the edge of the uncleared jarrah forest (*Eucalyptus marginata*). Road-killed *T. rugosus* were found regularly over most of the study area, but on the roads through the jarrah forest neither live nor dead *T. rugosus* were seen. Seven live *T. rugosus*, captured on the southeastern edge of the jarrah belt in country still containing extensive uncleared areas of forest, had no ticks attached to them. In the rest of the study area only two other uninfested *T. rugosus* were found (Figure 1).

Amb. albolimbatus is distributed along the south coast to the east and west of Albany (Figure 1), and abuts with, and may just overlap, *Ap. hydrosauri* about 6 km west and about 3 km east of Albany.

Discussion

It is not clear which factors prevent *Ap. hydrosauri* from spreading beyond its very narrow range around Albany. The morphologically similar species in South Australia occupies a wide range of environmental conditions (Smyth 1973). One environmental change which seems to have an important influence on the distribution of *Ap. hydrosauri* near Albany is the jarrah forest to the west. The density of *T. rugosus* appears to be lower there, and those found on the margins of the forest had no ticks on them. This suggests that some characteristic of the forest makes it unsuitable for occupancy by ticks.

The northern and eastern boundaries do not follow macroclimatic clines as does the boundary between *Ap. hydrosauri* and *Amb. albolimbatus* in South Australia (Smyth 1973). Near Albany the tick boundary crosses rainfall isoclines (Sharrad & King 1981). Moreover, *Ap. hydrosauri* is found in Western

Australia in areas receiving higher rainfall, such as south of Cape Naturaliste, and in areas receiving lower rainfall, such as Bremer Bay (Sharrad & King 1981).

There are no obvious vegetational changes at the northern and eastern boundaries. Much of the area has been cleared for farming, but wide roadside verges still maintain native vegetation classified as mallee heath (Beard 1976). There may be a subtle change, but if so it is not significant enough to show on the vegetation maps of the area (Beard 1976). In fact, *Ap. hydrosauri* does survive in the distinctly different and less mesic coastal scrub on drift sand dunes at Bremer Bay. (The Cape Riche and Bremer systems of Beard (1976).)

Topographic barriers are also unlikely to be important in maintaining the boundary. The area is dominated by two mountain ranges, the small Porongorup Ranges starting about 35 km north of Albany, and the more extensive Stirling Ranges starting about 65 km north of Albany (Figure 1). These ranges rise abruptly from the plains and there is a flat intermontane area, about 20 km wide, between them. At one point the boundary is located on this plain. The Woogenellup Road runs northeast from Mt Barker and along the southern edge of the Stirling Ranges; only *Amb. albolimbatus* is found along it. The Porongorup Road runs east from Mt Barker along the northern edge of the Porongorup Ranges; most lizards found along this road carried *Ap. hydrosauri*. Thus the boundary region must occur on the plain in between these roads; and the mountain ranges are not barriers to the extension of the range of either species. There are no topographic features of any significance along the eastern boundary of *Ap. hydrosauri*.

An alternative explanation is that the position of the boundary is independent of environmental gradients, but is maintained by an interaction between the species. The strength of this hypothesis is the lack of any other obvious options, although attempts to demonstrate interactions of ticks at other parapatric boundaries have not been successful (Bull *et al.* 1981). Nevertheless, the frequent occurrence of parapatric boundaries within this group of ticks (Bull *et al.* 1981) is circumstantial evidence in favour of the interaction hypothesis.

Perhaps *Ap. hydrosauri* was once distributed continuously from South Australia to southern Western Australia, but *Amb. albolimbatus* has subsequently spread and displaced it, to leave geographically isolated populations in eastern South Australia, in the southern part of Eyre Peninsula, and in a number of locations along the southern coast of Western Australia.

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RECENT NON-MARINE DOLOMITE FROM THE COASTAL PLAIN, SOUTHEASTERN SOUTH AUSTRALIA

BY CHRISTOPHER C. VON DER BORCH

Summary

The coastal plain of southeastern Australia has been the site for formation of a variety of carbonate minerals throughout the Quaternary. Dolomite and prodolomite (approximate chemical composition of dolomite but lacking in ordered reflections), magnesite, hydromagnesite, magnesian calcite and aragonite are presently forming in Holocene ephemeral lakes on portion of the coastal plain which is in close proximity to a modern coastal lagoon known as the Coorong. Radiocarbon dating has verified a modern age for at least some of these coastal dolomite occurrences. Pleistocene dolomitic carbonates have been detected in sediments from many interdunal depressions which lie between Pleistocene barrier islands remote from the present coast. These areas have been stranded by a combination of slow regional upwarp combined with eustatic sealevel fluctuations.

BRIEF COMMUNICATION

RECENT NON-MARINE DOLOMITE FROM THE COASTAL PLAIN,
SOUTHEASTERN SOUTH AUSTRALIA

The coastal plain of southeastern South Australia has been the site for formation of a variety of carbonate minerals throughout the Quaternary. Dolomite and protodolomite (approximate chemical composition of dolomite but lacking in ordered reflections), magnesite, hydromagnesite, magnesian calcite and aragonite are presently forming in Holocene ephemeral lakes on portion of the coastal plain which is in close proximity to a modern coastal lagoon known as the Coorong¹⁻⁵. Radiocarbon dating has verified a modern age for at least some of these coastal dolomite occurrences⁶. Pleistocene dolomitic carbonates have been detected in sediments from many interdunal depressions which lie between Pleistocene barrier islands remote from the present coast². These areas have been stranded by a combination of slow regional upwarp combined with eustatic sea-level fluctuations⁷⁻¹⁰.

The occurrence of the majority of active dolomite-forming lakes immediately adjacent to the present coastal lagoon suggested that proximity of a marine environment is a prerequisite for Coorong type dolomite formation. It was considered that the bulk of the necessary ions could be derived from a nearby marine reservoir, either from wind-borne cyclic salt² or by entrainment of seawater in coastal groundwater circulation. Subsequent hydrological and stratigraphic studies, however, have cast doubt on the necessity of a marine ionic source^{11,4}. To resolve the enigma, which has an important bearing on theories of dolomite genesis in the Coorong region, stratigraphic studies were initiated on Lake Ormerod, an inland, ephemeral, carbonate lake.

A series of shallow, ephemeral, carbonate lakes including Lake Ormerod occurs within a broad interdunal depression west of the town of Naracoorte. The lakes are situated approximately 85 km from the present coast at an elevation of 50 m above present sealevel. Based on palaeomagnetic dating¹⁰ this depression was at least in part a coastal lagoon about 600,000–700,000 years ago, but has since been separated from a marine environment by the regional upwarping and consequent regression.

In most aspects the inland lakes appear identical to their more numerous coastal counterparts. They are ephemeral in nature, filling with water during winter months by groundwater seepage and direct rainfall, and evaporating to dryness during ensuing arid summers. When full of water they are about 1 m deep and like their coastal counterparts support an abundant aquatic biota, including the aquatic grass *Ruppia maritima* and the small gastropod *Coriella confusa*. Some of the lakes are floored with fine-grained (0.2–14) dolomite mud. The purpose of this reconnaissance study is to define the age of the dolomite in these inland lakes using radiocarbon dating, in order to determine whether it could be forming at present or whether it is relict from times when a Pleistocene marine shoreline existed in the area.

A 1 m sediment core collected from Lake Ormerod comprises an uppermost 50 cm unit of white, fine-grained carbonate, shown by x-ray diffraction to be protodolomite (dolomite unit), overlying a dark grey organic-rich mud composed of calcite and subsidiary dolomite (calcite unit). Assuming that the dolomite is a primary form, this vertical mineralogical variation implies an environmental change from a pre-existing permanent swamp or lake to the present alkaline ephemeral lake, possibly in response to a decrease in rainfall during the past few thousand years.

Two samples from the top and bottom of the dolomite unit were selected for reconnaissance radiocarbon dating. The uppermost shows a ¹⁴C age of 1300 ± 60 years whilst the lowermost is 5770 ± 90 years (Table 1), proving that this lake at its surface contains modern and not Pleistocene dolomite. The age of the surface mud should be considered a maximum one. This anomalously old age could be due to a variety of factors, including dilution by reworking of older dolomite or formation from an admixture of "old" carbon derived by groundwater leaching of the underlying Pleistocene and Tertiary carbonate aquifers. The possibility also exists of a slow reaction rate, of the order of thousands of years, in the "penecontemporaneous" formation of dolomite in such a situation.

TABLE 1. Data tabulation for Lake Ormerod carbonate samples from reconnaissance borehole.

ANU Sample	Sample depth (cm)	Measured $\delta^{13}\text{C} \text{‰}$	% modern	$\Delta^{14}\text{C} \text{‰}$	Corrected age, years BP.
1419	0	-1.0 ± 0.2	85.0 ± 0.6	-149.8 ± 6.4	1300 ± 60
1470	50	-3.4 ± 0.2	48.8 ± 0.5	-512.2 ± 5.2	5770 ± 90

The modern age of dolomites in Lake Ormerod suggests that this mineral was formed a considerable time after sealevel regressed from the region. This implies that it must have formed from seasonally discharging Ca and Mg bicarbonate groundwaters of the unconfirmed regional

aquifer, and that proximity to a marine environment is not a necessary pre-requisite for genesis of this type of dolomite.

Radiocarbon dates were made at the ANU Radiocarbon Laboratory by Henry Polach.

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- ¹¹Von der Borch, C. C., Lock, D. E., & Schwebel, D. (1975). *Geology. May*, 283-5.

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FIRST RECORD OF PROMICROPS LANCEOLATUS (BLOCH) PISCES: SERRANIDAE) IN SOUTH AUSTRALIAN WATERS

BY P. J. KAILOLA AND G. K. JONES

Summary

Promicrops lanceolatus (Queensland Grouper or Sea Bass) is widespread through the tropical waters of the Indo-Pacific region, inhabiting lee and seaward sides of reefs and lagoons, as well as estuaries. The limits of its distribution have been reported as Algoa Bay (East Africa), India, Taiwan, Gilbert Islands, Fiji and Hawaii. In Australia it has been recorded from northern N.S.W., Queensland, Western Australia and “presumably N.T.”

BRIEF COMMUNICATION

FIRST RECORD OF *PROMICROPS LANCEOLATUS* (BLOCH) PISCES: SERRANIDAE) IN SOUTH AUSTRALIAN WATERS

Promicrops lanceolatus (Queensland Grouper or Sea Bass) is widespread through the tropical waters of the Indo-Pacific region, inhabiting lee and seaward sides of reefs and lagoons, as well as estuaries¹⁻². The limits of its distribution have been reported as Algoa Bay (East Africa), India, Taiwan, Gilbert Islands, Fiji and Hawaii³⁻⁴. In Australia it has been recorded from northern N.S.W., Queensland, Western Australia and "presumably N.T."⁵⁻⁶.

This account extends the southern distribution of the species and its presence in South Australia waters adds further support for a tropically-derived current occurring in southern Australian waters.

On 28.ix.1980, a fresh specimen of *P. lanceolatus* was washed up on the ocean beach of The Coorong (approx. 36°00'S, 139°30'E). It was taken to the South Australian Museum in Adelaide and a cast was prepared for the Museum. The specimen was retained there to recover its skeleton.

A description of the fish follows:

Family Serranidae. *Promicrops lanceolatus*

Holocentrus lanceolatus Bloch 1790, Nat. Auslând. Fische 4, p. 92, pl. 242, fig. 1 (reference copied).

S. Aust. Mus. cast, F.4562. Total length (TL) 2120 mm; standard length (SL) 1775 mm; Weight (fresh, intact) 153 kg.

D.XI, 16. A.III, 8. P.ii, 15, i. L.lat. about 61. Tr. 14 or 15+43 or 44. G.R. 8+1+8. The low

rakers anteriorly are difficult to distinguish from the rough platelets covering the gill arches. (Most authors credit *P. lanceolatus* with a gill raker count of 10+14+16. The anomaly here is remarkable. Randall⁷ found a lower-than-normal gill raker count for a 574 mm specimen of *Serranus fuscoguttatus* (Forsskål) and surmised that there is a loss of gill rakers in larger fish (Serranidae) because of fusion).

An irregular double series of stout teeth along each jaw is succeeded by bands of curved sharp teeth; bands of teeth also occur on vomer and palatines. The maxillary extends well past the eye, which is contained 3.7 times in the broad convex interorbital space. The middle opercular spine is slightly nearer the lower spine than to the upper. The 8th is the longest dorsal fin spine. The preoperculum is highly angular; soft fins are rounded.

Body colouration was dull dark brown, the fins somewhat darker and charcoal at their margins.

Gut contents were sand and grit, with several teleost vertebrae near the end of the intestines. Gonads could not be located.

Promicrops lanceolatus has been reported to grow to nearly 4 m long^{1,4,6}, and Schultz³ has investigated the authenticity of records of large-sized *Promicrops*. Specimens above 200 kg are known from the Hooghly River, India (TL 2.3 m, 209 kg)⁸; Thailand (TL 1.8 m, 216 kg)⁹; Bikini Atoll, Micronesia (TL 2.3 m, 214 kg; photograph at U.S. National Museum). The largest Queensland specimen reported weighed 288 kg¹⁰; Four-

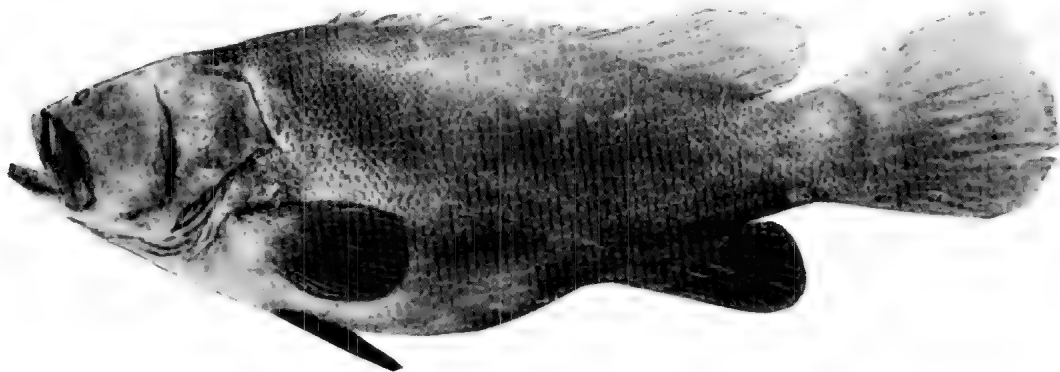


Fig. 1. Queensland Grouper *Promicrops lanceolatus*. Total length 2120 mm.

manoir & Laboute" state that *Promicrops* can reach 400 kg.

The South Australian specimen is believed to be the most southerly record for the species. Algoa Bay (approx. 34°00'S, 26°00'E) was the previous southerly record and this location is close to the southern-most limit of the tropical "Agulhas Current" which extends down the east coast of South Africa. Similarly, its discovery here can be explained by the presence of a current system originating from the tropical waters of the Indian Ocean. This current (the "Leeuwin Current") has been described¹²⁻¹⁴ as an eastward flowing current during autumn and winter months along the southern coast of Western Australia and across the Great Australian Bight. Satellite observations of sea surface temperature fronts¹⁵ show that this current of relatively warm, low salinity water flows completely across the Great Australian Bight. It is also interesting to note that Markina¹⁶ classified the phyto- and zooplankton in the Great Australian Bight as of tropical origin.

We thank Messrs. D. Wankie, A. Billing, D. Evans and D. Roberts who brought the fish to our attention and assisted with its transportation and measurements; also to Messrs. R. O. Ruehle and W. Head for the photograph and museum assistance.

TABLE 1. Measurements (in mm) of *P. lanceolatus* (obtained from the fresh specimen).

Total length	2120
Standard length	1775
Head length	730
Body depth	670
Snout length	170
Eye diameter	51
Interorbital width	190
Lower jaw tip to vent	1320
Maxillary length	390
Head depth	435
Caudal peduncle depth	215
Caudal peduncle length	345
Postorbital head length	510
Longest pectoral ray	360
Longest ventral ray	285
Longest anal ray	280
Third anal spine	111
Longest dorsal ray	250
Eighth dorsal spine	99
First dorsal spine	49
Last dorsal spine	80
Longest gill filament	69
Gill raker at angle	25

¹Roughly, T. C. (1951). 'Fish and Fisheries of Australia.' (Angus & Robertson: Sydney).

²Fourmanoir, P. & Laboute, P. (1976). "Poissons de Nouvelle Calédonie et des Nouvelles Hébrides." (Les Editions du Pacifique: Tahiti).

³Schultz, L. P. (1966). Addenda. p.p. 145-165. In: Schultz, L. P. & collaborators. U.S. natn. Mus. Bull. 202, 3.

⁴Smith, J. L. B. (1965). "The Sea Fishes of Southern Africa." 5th edn (Central News Agency: South Africa).

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⁷Randall, J. E. (1964). Pacific Sci. 18(3): 281-96.

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⁹Smith, H. (1933). J. Siam Soc. Nat. Hist. Suppl. 9(1): 85.

¹⁰Grant, E. M. (1978). "Guide to Fishes" (4th ed.) Dept Harbours & Marine, Qld.

¹¹Darbyshire, J. (1964). Deep-Sea Res. 11: 781-815.

¹²Rochford, D. J. (1975). Proc. Ecol. Soc. Aust. 8: 57-83.

¹³Pashkin, V. N. (1968). Tr. Atl. Nauchno-Issled. Inst. Rybu. Khoz. Okeanogr. 28 (transl.).

¹⁴Cresswell, G. R. & Golding, T. J. (1980). Deep-Sea Res. 27A: 449-66.

¹⁵Legeckis, R. & Cresswell, G. (in press). *Ibid.*

¹⁶Markina, N. P. (1976). Oceanology 15: 602-4.

HALO-EFFECTS IN NATIVE VEGETATION

BY ROBERT T. LANGE AND TIMOTHY REYNOLDS

Summary

Circular zones of suppressed growth, called halos, surround individuals and clumps of some plants, particularly trees such as *Casuarina cristata*, in South Australian vegetation. These halos extend well beyond the canopy spreads of the plants at their foci and show up clearly on aerial photographs. Suggested explanations of the suppression include water shortage induced by the central plant, allelopathy, or grazing and seed-harvesting animals harboured by the central plant, but field observations indicate that none of these provides a satisfactory explanation on its own.

BRIEF COMMUNICATION

HALO-EFFECTS IN NATIVE VEGETATION

Circular zones of suppressed growth, called halos^{1,2}, surround individuals and clumps of some plants, particularly trees such as *Casuarina cristata*, in South Australian vegetation. These halos extend well beyond the canopy spreads of the plants at their foci and show up clearly on aerial photographs. Suggested explanations of the suppression include water shortage induced by the central plant, allelopathy, or grazing and seed-harvesting animals harboured by the central plant, but field observations indicate that none of these provides a satisfactory explanation on its own³.

Zones of enhanced growth also occur, particularly under trees such as *Acacia papyrocarpa* and shrubs such as *Maireana sedifolia*. These zones usually do not spread beyond the canopies of their producers, and do not show up on aerial photographs, but are obvious to the ground observer. Suggested explanations for the enhancement include soil³ and microclimate⁴ conditions induced by the central plant and, under intricate shrubs, protection from the grazing of large vertebrates⁴, yielding contrasts with unprotected interspaces. In general field observations support the view that these are very plausible hypotheses, but there are complications. For instance *A. papyrocarpa* canopies in the Whyalla region usually enhance the likelihood of finding species beneath them, and lack an extended grass suppression halo, but sometimes the reverse is observed. Both categories of zones are well known elsewhere⁵⁻⁹. The most recent Australian publication about them concerns *Eucalyptus baxteri* suppression zones in Victorian tree-heath¹⁰.

We have detected a further category of such plant-centred effects which, so far as we can establish, is unreported. It differs from the preceding in that it is not expressed as overt general suppression or enhancement of plant growth around particular trees or shrubs, and cannot be proved by inspecting any single tree or shrub for halo effects. The effect is proved only by considering the species population collectively and consists of tendencies, within small circles centred on individuals, for halos of shifts in floristic composition of surrounding vegetation, i.e. for shifts in the probabilities of incidence of other species, from those applying within small circles centred on individuals of a species to different probabilities applying in the interspaces between the circles. This note summarizes our investigation and its findings.

Traverses in native vegetation were marked out separately between individuals of each species under test for halo-effect. Our technique required successive individuals to be separated by a least twice their canopy diameter.

Circles of radius r_1 , r_2 ... r_{10} (r in the range 0.5–3.0 m) were marked out around each indi-

vidual of a test species and searched for incidence of all other species. This was repeated at a random point in each midlocation between test individuals. Data for each quadrat size separately were assembled as 2×2 homogeneity tables for each combination of test and other species in turn, and tested for significance by χ^2 or Fishers exact test¹¹, using a computer. Results were graphed as

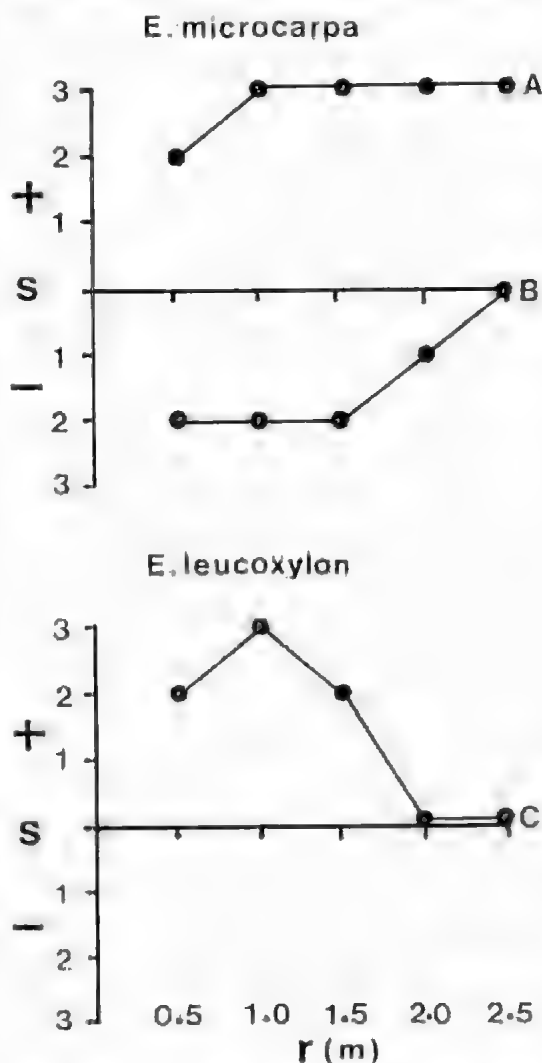


Fig. 1. Halo signatures of *Eucalyptus microcarpa* and *E. leucoxylon* in native vegetation at Belair. Individuals of these species were intermingled as tree cover over dense, low sclerophyllous scrub. 3 = the significance level of $p \leq 0.001$. + and - signify positive and negative associations respectively, A = *Acrotriche serrulata*, B = *Gonocarpus elatus*, C = *Olea europea*.

in Figure 1 to display the "signature" of the halo effect. We also examined association patterns arising from 4 m square quadrats distributed randomly through the same vegetation.

We applied these techniques in local relict native vegetation of the sort that the National Parks and Wildlife Act aims to preserve. Findings were as follows:

(1) Various native species had halo effects expressed only as shifts in the probability of incidence of other species within the halo of the test species. These shifts involved both increased and decreased probabilities simultaneously. Various other species lacked such effects.

(2) Most of these effects were not detected by large quadrats scattered randomly in the vegetation, which explains why they seem to have been overlooked in earlier plant sociological studies.

(3) Some halo-producing species intermingled in the one habitat have equivalent habit (e.g. *Eucalyptus microcarpa* and *E. leucoxylon* in layered woodland at Belair) but have different signatures (Figure 1), indicating species-specificity beyond single-cause explanations such as bulk inhibition or enhancement by waterstress or shade.

(4) Perennial weeds, which are a main cause of degradation in heritage vegetation, are caught up in these effects. In woodland near Belair, *Asparagus asparagoides* (bridal creeper) was positively associated with small clumps but not separated individuals of *Exocarpus cupressiformis*. *Rhamnus alaternus* (buckthorn) and *Olea europea* (olive) seedlings were highly associated with the halo of *Eucalyptus leucoxylon* (blue gum) (Figure 2), but not of *E. viminalis* (manna gum), *E. camaldulensis* (river gum), *E. fasciculosa* (pink gum) or *E. microcarpa* (peppermint). To that extent blue gum represents a "weak link" in such heritage vegetation, and the replacement of some foothills

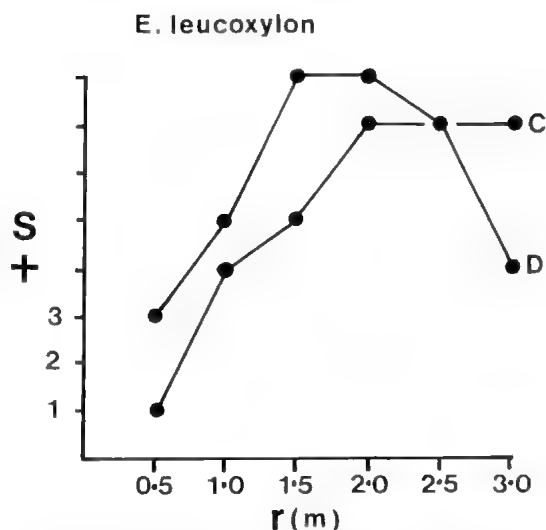


Fig. 2. Halo effect of *Eucalyptus leucoxylon* on *Olea* (C) and *Rhamnus* (D) in native vegetation at Black Hill. Other legend as in Figure 1.

native woodland by olive woodland probably was fostered by this link, for which no explanation is available. Once established, olive harbours its own seedlings.

(5) There is evidence that some native sub-shrubs interact negatively with some weeds. This encourages the view that thorough screening might reveal natives with halo suppression of weeds sufficient to warrant their evaluation for reclamatory and buffer planting.

In conclusion, we think that this evidence points to a neglected but important feature of patterning in native vegetation, with scope for practical applications, and which demands the formulation of convincing explanations.

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²Johnson, A. W. (1978). Vegetation suppression in the Whyalla region, with particular reference to the phenomena around *Casuarina cristata* Miq. B.Sc. (Hons) Thesis, Department of Botany, University of Adelaide.

³Correll, R. L. (1966). Studies on the nitrogen economy of semiarid vegetation at Yudnapinna Station, South Australia M.Sc. Thesis, University of Adelaide.

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South Australia. Ph.D. Thesis, University of Adelaide.

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⁷Jaksic, F. M. & Fuentes, E. R. (1980). J. Ecol. 68, 665-70.

⁸Storey, R. (1967). Aust. J. Bot. 15, 175-87.

⁹Nat. Acad. Sci. (1971), "Biochemical Interactions among plants." Environmental Physiology Subcommittee. (Washington D.C.).

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¹¹Sokal, R. R. & Rohlf, F. (1969). Biometry. W. H. Freeman Co., N.Y.

NOTES ON REPRODUCTION BY CAPTIVE AMPHIBOLURUS NULLARBOR (SAURIA: AGAMIDAE)

BY JULIA SMITH AND TERRY D. SCHWANER

Summary

Two *Amphibolurus nullarbor* Badham were collected 20 km E of Nullarbor Homestead, S.A. (31°28'S, 131°12'E), amongst bluebush (*Maireana sedifolia*) on the Nullarbor Plain (above the cliffs) by S. Doyle on 30.viii.1980. Abdomens of both females were distended and oviducal eggs were easily palpable. One specimen (S.A.Mus. R18170, SVL=140 mm) was preserved; dissection revealed six shelled eggs in the right oviduct and eight in the left. Because reproduction in this species has not been reported, the other lizard (SAM R18581, SVL=135 mm) was kept alive until parturition to document clutch size, egg sizes during incubation, hatching times and hatching sizes under laboratory conditions.

BRIEF COMMUNICATION

NOTES ON REPRODUCTION BY CAPTIVE *AMPHIBOLURUS NULLARBOR* (SAURIA: AGAMIDAE)

Two *Amphibolurus nullabor* Badham were collected 20 km E of Nullarbor Homestead, S.A. (31°28'S, 131°12'E), amongst bluebush (*Maireana sedifolia*) on the Nullarbor Plain (above the cliffs) by S. Doyle on 30.viii.1980. Abdomens of both females were distended and oviducal eggs were easily palpable. One specimen (S.A.Mus. R18170, SVL=140 mm) was preserved; dissection revealed six shelled eggs in the right oviduct and eight in the left. Because reproduction in this species has not been reported, the other lizard (SAM R18581, SVL=135 mm) was kept alive until parturition to document clutch size, egg sizes during incubation, hatching times and hatching sizes under laboratory conditions.

On 1-2.x.80, 12 eggs were found scattered in the vivarium enclosure. Each egg was measured, marked for identification, and placed on damp aquarium gravel in a clear plastic container loosely covered with plastic wrap. The container was placed on top of a refrigerator, near the back, where the temperature was 27-29°C¹⁻³. Water was sprayed on the eggs weekly to prevent dessication. Three eggs became mouldy within the first month of incubation and were discarded. Two additional eggs were laid on 8.x.80; these were preserved in formalin (R18581-eggs).

Egg sizes measured at different times during incubation indicated an average increase in egg volume of 83% (computed as the volume of an ellipsoid from differences between initial and maximum egg sizes, Table 1). Most eggs decreased slightly in length and/or width just prior to hatching (compare size data for 11/13 and 12/14, Table 1).

Hatchlings emerged 18-27.xii.80, after 79-80 days incubation. Neonates remained in the eggs for 2-16 hr with only their heads protruding. Three lizards left the eggs with parts of the yolk sac still visible but the yolk was absorbed 2-3 hr after full emergence. Hatchlings ranged 33.6-37.3 mm ($X=35.9\pm1.1$ mm) SVL and 75.6-87.5 mm ($X=81.9\pm4.3$ mm) total length. There was no significant correlation ($r=.04$, $n=9$) between hatching SVL and maximum egg volume (computed as before from Table 1). Colour and pattern of the young (Fig. 1) were similar to that of adults⁴⁻⁵.



Fig. 1. Hatchling *Amphibolurus nullabor*; SVL=37.3 mm.

TABLE 1. Egg sizes (length and width in mm), hatching dates, and hatchling sizes (SVL and total length in mm) for a clutch of *Amphibolurus nullabor* eggs.

Egg no.	Dates Measured (1980)				Dates hatched (Dec. 1980)	Hatchling sizes	
	10/1-2†	10/28	11/13	12/14*		SVL	TL
1	22.9 x 13.9	24.7 x 17.4	26.0 x 18.6	26.1 x 19.1	19	36.3	85.3
2	23.4 x 14.6	26.1 x 17.0	27.1 x 18.3	26.6 x 17.9	21	37.0	87.5
3	24.2 x 15.8	26.6 x 17.9	27.6 x 19.4	26.9 x 20.0	22	36.3	83.2
4	23.5 x 15.0	26.2 x 18.4	27.6 x 19.3	24.9 x 19.2	18	37.3	80.0
5	23.0 x 15.3	23.2 x 18.1	26.1 x 19.1	25.1 x 19.1	21	35.9	86.1
6	23.8 x 15.6	26.3 x 18.7	27.0 x 19.3	26.0 x 18.2	25	33.6	75.6
7	23.8 x 14.4	26.0 x 18.0	26.7 x 18.7	26.6 x 18.9	27	35.6	76.0
8	22.9 x 16.1	24.8 x 17.9	25.6 x 18.7	24.2 x 18.9	24	35.0	80.2
9	24.0 x 14.2	24.8 x 17.9	26.4 x 18.6	25.8 x 18.4	20	36.1	82.8
X ± SD	23.5 15.0 ±0.5 ±0.8	25.0 17.9 ±1.1 ±0.5	26.7 18.9 ±0.7 ±0.4	25.8 18.9 ±0.9 ±0.6		35.9 ±1.1	81.9 ±4.2

† Dates when eggs laid.

* Note that all eggs except No. 1 decreased in length and/or width just prior to hatching.

These observations are similar to those reported for *A. barbatus*, which most resembles *A. nullarbor*, morphologically⁴. Eggs of *A. barbatus* increased 90% by volume from parturition to maximum size, under incubation conditions similar to those described here⁶. Also *A. barbatus* eggs shrank slightly just prior to hatching, and hatchlings remained motionless in ruptured eggs for several hours⁶. Furthermore, hatching times (76–84 days) for a clutch of *A. barbatus* eggs from Queensland, incubated at a similar temperature, were similar to the *A. nullarbor* data⁶.

In S.A. populations of both species are allopatric⁵. Parturition seems to occur slightly earlier for *A. nullarbor* (early October) than for *A. barbatus* (late October, with most clutches reported in November–December^{2, 7}). This difference

may be related to the more northerly distribution of *A. nullarbor* populations in S.A., which experience the seasonal effects of exogenous stimuli (longer photoperiod and increasing temperatures) favourable to the onset of gonadal cycles⁸ earlier than populations of *A. barbatus*. Clutch sizes are much smaller for *A. nullarbor* (14–16 eggs for the two females examined) than for *A. barbatus*, which lay 15–35 eggs per clutch ($X=25\pm6$ for six observations from S.A.^{2, 8}, and often have two clutches per season^{2, 6, 8}). Snout-vent lengths for hatchling *A. barbatus* average 5 mm larger than those of *A. nullarbor*. These differences are believed to be related to differences in body size of adults (maximum SVL 141 mm for *A. nullarbor* compared with 220 mm in *A. barbatus*)⁶.

Roman Ruehle photographed the hatchling *A. nullarbor*.

¹Bustard, H. R. (1979) Australian Lizards. Collins, Sydney, 162 pp.

²Smith, J. (1974). S. Aust. Herpetol., 2(1): 10.

³Smith, J. (1979). Herpetofauna, 19(2): 12–14.

⁴Badham, J. A. (1976). Aust. J. Zool., 24: 423–443.

⁵Houston, T. F. (1979). 'Dragon lizards and goannas of South Australia.' S. Aust. Mus. Spec. Ed. Bull. Ser., 84 pp.

⁶Bustard, H. R. (1966). Brit. J. Herpetol., 3: 252–259.

⁷Licht, P. (1973). Comp. Biochem. Physiol. 45A: 7–20.

⁸Mitchell, F. J., unpublished data.

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SKULLS OF BETTONGIA LESUEUR (MAMMALIA: MACROPODIDAE) FROM A CAVE IN THE FLINDERS RANGES, SOUTH AUSTRALIA

BY MEREDITH J. SMITH AND P. A. W. ROGERS

Summary

Many Australian mammal species suffered a drastic reduction of range and some became extinct soon after European colonization. Information on the former distribution of these species can be obtained only opportunistically by the discovery and recognition of their remains in protected locations such as caves, dunes and middens.

SKULLS OF *BETTONGIA LESUEUR* (MAMMALIA: MACROPODIDAE) FROM A CAVE IN THE FLINDERS RANGES, SOUTH AUSTRALIA

Many Australian mammal species suffered a drastic reduction of range and some became extinct soon after European colonization. Information on the former distribution of these species can be obtained only opportunistically by the discovery and recognition of their remains in protected locations such as caves, dunes and middens.

During the exploration of Yellowfooted Rock Wallaby Cave (lat. 31°20'S, long. 138°40'E), about 30 km north of Wilpena in the Flinders Ranges, South Australia one of us (P.R.) found two macropodid skulls and a pelvis in a low tight passage some distance from the entrance to the cave. The topography of the cave indicated that there was little likelihood of the bones having been carried to their resting place by a water current.

The more complete skull (now registered South Australian Museum) (SAM M10769) lacks left U and a few fragments of the premaxillae. The lower jaw and the anterior cervical vertebrae are held tightly in place by dry flesh and skin, and fragments of dry skin and fur adhere to the skull. The other skull (SAM M10770) lacks the incisors and anterior parts of the nasal bones. It has no skin adhering but is greasy. The pelvis and attached lumbar vertebrae have ligaments and dried flesh adhering; they seem to have been gnawed by rodents.

Both skulls are of adult *Bettongia lesueur* (Quoy & Gaimard) and the pelvis is almost certainly of this species. *B. lesueur* is characterized by vertically-grooved, very long premolars, low-crowned bunodont molars, steep size gradient of molars with M¹ very small, and by inflated auditory bullae. The P⁴ length is about 14% of basal length of skull, the bulla length about 25% of basal length¹. For the two cave skulls the measurements in mm relevant to diagnosis are: basal length 63.0, approx. 63; P⁴ length 8.9, 8.9; bulla length 17.6, 17.8 respectively.

B. lesueur was widespread in Australia and as late as 1940 was abundant in the Musgrave-Everard Range area² although it exists now only on offshore islands in Western Australia³. Eidsen⁴ found "abundant evidence to show that *Bettongia lesueur* was formerly one of the most numerous and universally distributed mammals of South Australia, finding and colonizing suitable habitat zones in all the districts of the State with the possible exception of the deeper Mallee and the flooded portion of the lower South-East and the inner portions of the Nullarbor Plain". His broad outline of the distribution included all of

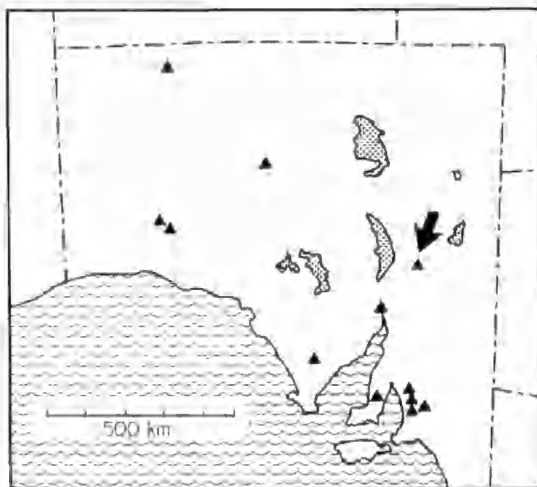


Fig. 1. Map of South Australia showing location of origin of specimens of *B. lesueur* in the South Australian Museum mammal collection. Arrow shows Yellowfooted Rock Wallaby Cave.

South Australia except the far northeast. However, few specimens were retained in museums. In the South Australian Museum there are no specimens of *B. lesueur* from the Flinders Ranges, the nearest locality being Pt Augusta, where one specimen (M9093) was taken in 1880 (Fig. 1) and living specimens have not been recorded from the Flinders Ranges⁵. A mandible fragment of *B. lesueur* has been found in an owl pellet deposit in Chambers Gorge, northern Flinders Ranges (G. C. Medlin, personal communication).

The rocky habitat around Yellowfooted Rock Wallaby Cave is not typical for *B. lesueur*, individuals of which are burrowers, and live in warrens dug in sandy soil¹. Whilst the small areas of alluvial sand deposited in the gorges by Enorama and Brachina Creeks may have provided some suitable substrate for burrowing, the position of the bones deep within a small cave suggests that caves as well as burrows were used for shelter. It is unlikely that the specimens from the cave lived elsewhere than in the Ranges because the plains to the west are about 19 km distant and to the east further away.

Whilst dried flesh may survive on bones in a cave for thousands of years⁶ the skulls from Yellowfooted Rock Wallaby Cave provide a positive record of *B. lesueur* from the Flinders Ranges in the late Holocene.

¹Wakefield, N. A. (1967). *Viet. Nat.* 84, 8-22.

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³Ride, W. D. L. (1970). "A guide to the native mammals of Australia". Oxford University Press, Melbourne.

⁴Ailken, P. F. (1980). Mammals, pp. 288-314 in Corbett, D. ed., "A Field Guide to the Flinders Ranges." Rigby, Adelaide.

⁵Partridge, J. (1967). *J. R. Soc. W. Aust.* 50, 57-59.

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A GIANT DEEP-SEA SQUID, TANINGIA SP., FROM SOUTH AUSTRALIAN WATERS

BY WOLFGANG ZEIDLER

Summary

In April 1980 fishermen from Port Lincoln reported the capture of a giant squid bearing hooks instead of suckers on the arms. The specimen, estimated to be 2 m long x 1.5 m wide, was floating on the surface 120 km offshore, south of Port Lincoln. Unfortunately the boat from which the discovery was made did not have the facilities to keep the specimen whole, and so it was cut up and subsequently sold for bait. However, two arms and the beaks were recovered, thus permitting generic identification.

BRIEF COMMUNICATION

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In April 1980 fishermen from Port Lincoln reported the capture of a giant squid bearing hooks instead of suckers on the arms. The specimen, estimated to be 2 m long x 1.5 m wide, was floating on the surface 120 km offshore, south of Port Lincoln. Unfortunately the boat from which the discovery was made did not have facilities to keep the specimen whole, and so it was cut up and subsequently sold for bait. However, two arms and the beaks were recovered, thus permitting generic identification.

Dismay at the destruction of such a scientifically valuable specimen prompted fishermen to look out for more and, in early May, 1980 two were recovered from the same general area. One of these had the head and arms missing, but still weighed 95 kg and had a dorsal mantle length of 158 cm. The other specimen weighed in excess of 110 kg and measured 2.1 m total length. It was in almost perfect condition and is currently frozen awaiting a more detailed examination.

Preliminary investigations have shown that the specimens represent the genus *Taningia* (Family: Octopoteuthidae), but as they have not been examined in detail a specific determination could not be made. However, they are most likely *T. danae* Joubin, 1931, as the genus is monotypic and the material at hand does not seem to vary markedly from published descriptions¹⁻³.

There are a number of distinctive features which characterize this species. The arms are relatively short, about $\frac{1}{4}$ of the mantle length and are armed with a series of hooks instead of suckers. The second arms each bear a large light organ at their tip which was bright yellow in the present specimens and measured about 5 x 3 cm. The tentacles, which account for most of the length in the true giant squids, *Architeuthis*, are absent in mature specimens and vestigial in juveniles of *Taningia*. The fins extend for most of the mantle and are

very large, making the body of the animal almost as broad as the mantle length. The mantle wall and fin are extremely thick and gelatinous and the body is relatively more bulky than any other species of squid.

Nearly all of the known specimens of *Taningia* have been collected from sperm whale stomachs, and it is unusual to encounter them floating on the surface. It is possible that they were regurgitated by sperm whales, and this may be the case for the specimen lacking a head, but the other two were found in relatively good condition and the fishermen estimated that they had died only very recently. According to the Port Lincoln fishermen dead squid often come to the surface near the edge of the continental shelf, but they are quickly eaten by seabirds and it is difficult to find a complete specimen. *T. danae* forms an important part of the diet of sperm whales and by weight is the most significant part of sperm whale diets³. Clarke⁴ recorded beaks and portions of flesh of this species from the stomachs of sperm whales caught near Albany, W.A., but this is the first definite record of *Taningia* from Australian waters. The previously known distribution of *Taningia*, mainly from sperm whale stomachs, includes the Azores, Madeira, the equatorial Atlantic and the eastern coast of South Africa².

I intend to publish the results of a more detailed examination of the specimens in the near future.

My sincere thanks to Dinko Lukin and the crew of the "Katina G" and to Juergen Zenke and the crew of the "Rosalind Star" for collecting and donating the specimens to the South Australian Museum. My thanks also go to S.A.F.C.O.I., who transported the specimens to Adelaide free of charge. A special thanks is due to Neville Wanklyn of the "Port Lincoln Times" who alerted the fishermen to the importance of the specimens, and to his Editor for being so understanding.

¹Joubin, L. (1931). *Annls Inst. oceanogr.*, Monaco 10, 169-211.

²Clarke, M. R. (1967) *Symp. zool. Soc. Lond.* (19), 127-43.

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ADDENDUM

BUTLER & KEOUGH—*Trans. R. Soc. S. Aust.* 105(1), 29-39.

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